THE EFFECT OF TORPOR ON PULMO-CUTANEOUS WATER LOSS IN *Perognathus parvus*.

by

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ABSTRACT

Studies were conducted to determine the effect of torpor on the pulmo-cutaneous water loss of a small, fossorial desert rodent, Perognathus parvus. Since the pulmonary and cutaneous components of the water budget are strongly affected by ambient temperature and humidity, these losses are extremely important in determining the ability of an animal to maintain positive water balance.

Simultaneous measurements of pulmo-cutaneous water loss and metabolic rate were made over a range of ambient temperatures of 10-35 C for both torpid and normothermic animals. Additional experiments were conducted to determine the ratio of pulmonary to cutaneous water loss, and to determine the relationship of these losses to ambient temperature. Models of energy budgets and water budgets were constructed to assist in determining the effect of variable amounts of torpor over the range of ambient temperature of 0-30 C.

It was found that normothermic animals could maintain positive water balance from 0-20 C at 0% relative humidity, but torpid animals were always in negative water balance under the same conditions. The inability of torpid animals to maintain positive water balance is attributed to the necessity of balancing the relatively fixed cutaneous loss against the much-reduced metabolic water production. It is concluded that torpor cannot serve as a water-conserving mechanism in this species at 0% relative humidity.

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INTRODUCTION

The physiological adaptations of desert animals, particularly the water-conserving adaptations, have interested scientists for decades. Schmidt-Nielsen and Schmidt-Nielsen, and their associates, stimulated much additional research in this field with their work beginning in 1948 and continuing to the present. The earlier literature was adequately reviewed by Schmidt-Nielsen and Schmidt-Nielsen (1952) and will not be repeated here in detail. Other good reviews of various facets of the problem of adaptation to desert environments are those of Schmidt-Nielsen (1964 a, b), Hudson (1964), Hudson and Bartholomew (1964), and Chew (1961, 1965).

The phenomenon of hibernation-aestivation has also attracted much interest, and the literature on this topic is truly voluminous; recent reviews of this literature are those of Kayser (1961), Lyman and Chatfield (1955), Lyman (1961), and Hayward (1967).

As Schmidt-Nielsen and Schmidt-Nielsen (1951) pointed out, the water balance of desert rodents is highly dependent upon metabolic rate, since the intake of water, production of metabolic water, and loss of water through evaporation and urine are all necessarily related to metabolic rate. It is a well-documented fact that some desert rodents exhibit a summer torpor, or

aestivation, which results in drastic reduction in metabolic rate. Many authors have assumed that aestivation is useful for water conservation. This assumption is exemplified by the comment of MacMillen (1965): "Thus it appears certain that cactus mice aestivate in their burrows during the summer, employing torpor as a water-conserving device ....". The nature of the problem is stated clearly by Hudson and Bartholomew (1964):

> "The correlation between hot dry seasons and the incidence of estivation generally has been used as ipso facto evidence that a lack of moisture may induce summer torpidity.
>
> "It may be argued that the reduction in the resting metabolism of estivators is an adaptation for coping with high ambient temperatures when the small gradient of body temperature to air temperature limits the rate of heat loss. This reduction in metabolism entails a reduction in metabolic water production which is at least partly counteracted by a reduction in respiratory water loss. Since these factors are in unknown proportions, a reduced metabolism may or may not be particularly advantageous to the water economy ...."

This thesis occupies a position at the cross-roads of these two main lines of research, desert adaptation and torpor, and its main objective is to determine the magnitude of the

various components of the water budget so that the effects of torpor on the water budget can be evaluated. This information is not available in the existing literature.

The experimental animal used for this study was Perognathus parvus, the Great Basin pocket mouse, which reaches the northern limit of its geographical distribution in the Osoyoos Arid Zone in British Columbia. Like most heteromyids, P. parvus can survive indefinitely on a diet of dry seeds. The members of the genus can produce a very concentrated urine, have a low insensible water loss, and have the ability to become torpid at environmental temperatures below body temperature. A comparison of physiological data for various species of Perognathus with similar data for other desert rodents indicates that the sub-family Perognathinae is as well adapted for desert environments as other nocturnal, fossorial rodents, such as Dipodomys. Persons interested in descriptions of the range, type of habitat, and gross morphology of the species are referred to Iverson (1967).

This thesis will be devoted to the collection of data of energy expenditure and insensible water loss (pulmo-cutaneous water loss) over the range of environmental temperatures encountered in the field, in order to test the following hypothesis: Torpor will not reduce the net water loss of Perognathus parvus, a typical small desert rodent, at ambient temperatures of 0 to 30 C and at 0% relative humidity.

MATERIALS AND METHODS

Experimental Animals

The animals for this study were obtained from the low areas at the north-east end of Lake Osoyoos. Longworth traps were set in a grid pattern. Trap success varied from 5% to 50% with an average of about 30%. Animals were held in mesh-covered metal jam tins stacked in cardboard boxes in an air-conditioned motel room until the collection was complete. Lettuce and sunflower seeds were provided daily. There was little or no mortality under these conditions.

The animals were maintained in the laboratory on a diet of sunflower seeds (ad lib.). The photoperiod in the animal room was 16 hr light and 8 hr dark. Humidity was about 50% and temperature was about 20 C.

Metabolic Rate and Pulmo-cutaneous Water Loss

Oxygen consumption, carbon dioxide production, and pulmo-cutaneous water loss were measured simultaneously in a closed-system respirometer similar to that used by Schmidt-Nielsen and Schmidt-Nielsen (1950). A pump circulated air through the system at approximately 500 ml per minute. Pulmo-cutaneous water was absorbed by two tubes of Drierite. Carbon dioxide was absorbed by a tube of Lithasorb. Both water loss and carbon dioxide production were determined by weighing the tubes to the nearest 0.1 mg. A spirometer recorded the oxygen consump-

tion on a kymograph, the oxygen being replenished automatically by a solenoid valve on an oxygen cylinder. The animal chamber, a one-liter jar, was submerged in a water bath to maintain constant temperature. In normal operation, the animal was placed in the jar over a pan of mineral oil and allowed to remain for at least one hour before data were collected. The length of a measurement was usually one hour, but one-half hour periods were used in some cases. Oxygen and carbon dioxide values were converted to standard temperature and pressure before metabolic rate and respiratory quotient were computed.

Pulmonary : Cutaneous Ratio of Evaporative Water Loss

Ten measurements of the pulmonary:cutaneous water loss ratio were made. A special double-compartment chamber was constructed with a rubber diaphragm separating the compartments. The animal was placed in the chamber with its head through a hole in the diaphragm, effecting a separation of "head skin + pulmonary" evaporative water loss from the "body skin" evaporative water loss. Two pumps and two separate water-absorbing tubes were used. Since these animals resist such confinement, it was necessary to tranquilize them with Tranimal (Hoffman - LaRoche) prior to the measurements. Other procedures were the same as for normal operation.

Cutaneous Water Loss and Total Surface Area

Cutaneous water loss was measured on 7 animals.

Technical problems involving the separation of pulmonary and cutaneous losses prevented the use of live animals for this experiment. The animals were killed by an overdose of Nembutol (i.p.). Each animal was placed in the metabolism chamber, and cutaneous water loss was measured at half-hour intervals. Each animal was tested at three different ambient temperatures, typically at 10, 20, and 30 C.

After the cutaneous loss was measured, the animal was removed from the chamber and weighed. The hair was removed with a depilatory cream, and a thin layer of silicone rubber was applied to the entire body surface. After the rubber had cured, it was peeled off the body in one piece. The rubber skin was traced on heavy cardboard, and surface area was determined by weighing the cardboard.

Metabolic Rate During Arousal From Torpor

All systems used in this experiment were as described previously. A torpid animal was selected, and after its deep body temperature had been taken with a thermistor probe through the abdominal wall, it was placed in the respirometer as quickly as possible. Oxygen consumption was recorded until the onset of shivering, usually about 10 to 15 minutes. The oxygen consumption for the remainder of the 30-minute test period was recorded separately by switching to a new set of tubes when shivering was observed. At the end of the test

period the animal was removed and the deep body temperature was taken as described. The total calories required for arousal were calculated by multiplying the total amount of oxygen used, by the caloric equivalent of oxygen at the observed R. Q. (respiratory quotient).

Data Analysis

The data were punched on computer cards and examined for meaningful linear relationships by least squares regression.

Construction of Energy Budget

A model for weekly energy expenditure was constructed using two independent variables, "hours in torpor per week" and "ambient temperature". The time required for entering torpor was assumed to be constant since the variation with temperature seems to be relatively small for all ambient temperatures between 10 and 30 C. The time required for arousal is a function of ambient temperature. To simplify the model, it was assumed that entry and arousal occur, even at zero hours of torpor. The least-squares regression equations for metabolic rate for the active and the torpid states were used in constructing the model.

Total time in torpor per week was varied from 0 to 140 hours. Ambient temperature (T_A) was varied from 0 to 30 C. Body weight and number of periods of torpor per week were introduced as constants. The computer

produced three-dimensional plots of the model for each selected combination of body weight and number of torpor periods per week.

Construction of Water Budget

The same independent variables and constants used in the energy budget were used also in the construction of a model for weekly water loss. Metabolic water is dependent upon diet, so it is necessary to construct a model for each diet considered. Since Schmidt-Nielsen's calculations (1951) were based on a diet of pearl barley, it was desirable to use that diet in the model to facilitate comparisons with his data. Three-dimensional plots of this model were prepared by computer as described for the energy model.

RESULTS

Energy Requirements

All metabolic rates reported in this thesis are resting metabolic rates of post-absorptive animals. Thus, at thermal neutrality, the metabolic rate reported is the "basal",or standard, metabolic rate.

The linear regressions of metabolic rate over a range of ambient temperatures are shown for non-torpid (normothermic) animals in Fig. 1 and for torpid animals in Fig. 2. The regression for non-torpid animals was based on data only up to 30 C to avoid the non-linear portion of the curve. The extrapolation of this line intersects the X-axis at 36 C. The mean body temperature of 10 normothermic mice was 35.4 C. To obtain an accurate estimate of the thermoneutral zone, additional measurements of metabolic rate were made at small intervals of T_A (ambient temperature) over the range of 25 to 35 C. The resulting curves for 8 individuals are shown in Fig. 3. The mean thermoneutral point (32 C) and the mean metabolic rate at 35 C from these data were used to extrapolate the metabolic rate curve above 30 C in Fig. 1. The slope of the metabolic rate regression in Fig. 1 was significantly different from zero at the 0.01 level of significance. The slope of the regression in Fig. 2 was significantly different from zero at the 0.05 level. Since the probability of obtaining these slopes by chance is less than 5%, we may

FIG. 1

RELATIONSHIP OF METABOLIC RATE TO AMBIENT TEMPERATURE

Y = 8.606 - 0.2397X N = 84

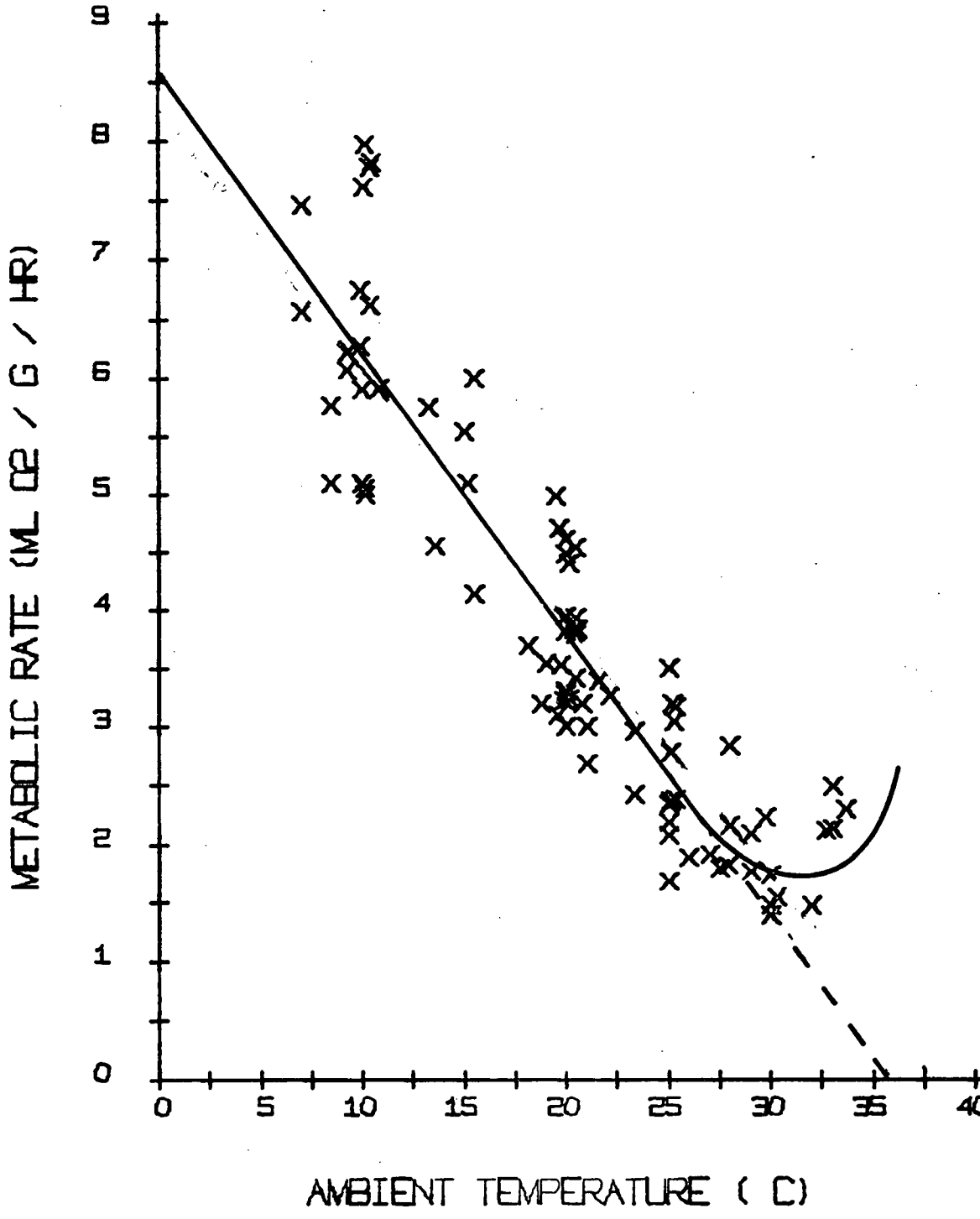


FIG. 2

RELATIONSHIP OF METABOLIC RATE OF TORPID ANIMALS TO AMBIENT TEMPERATURE

Y = 0.3841 + 0.0144X N = 32

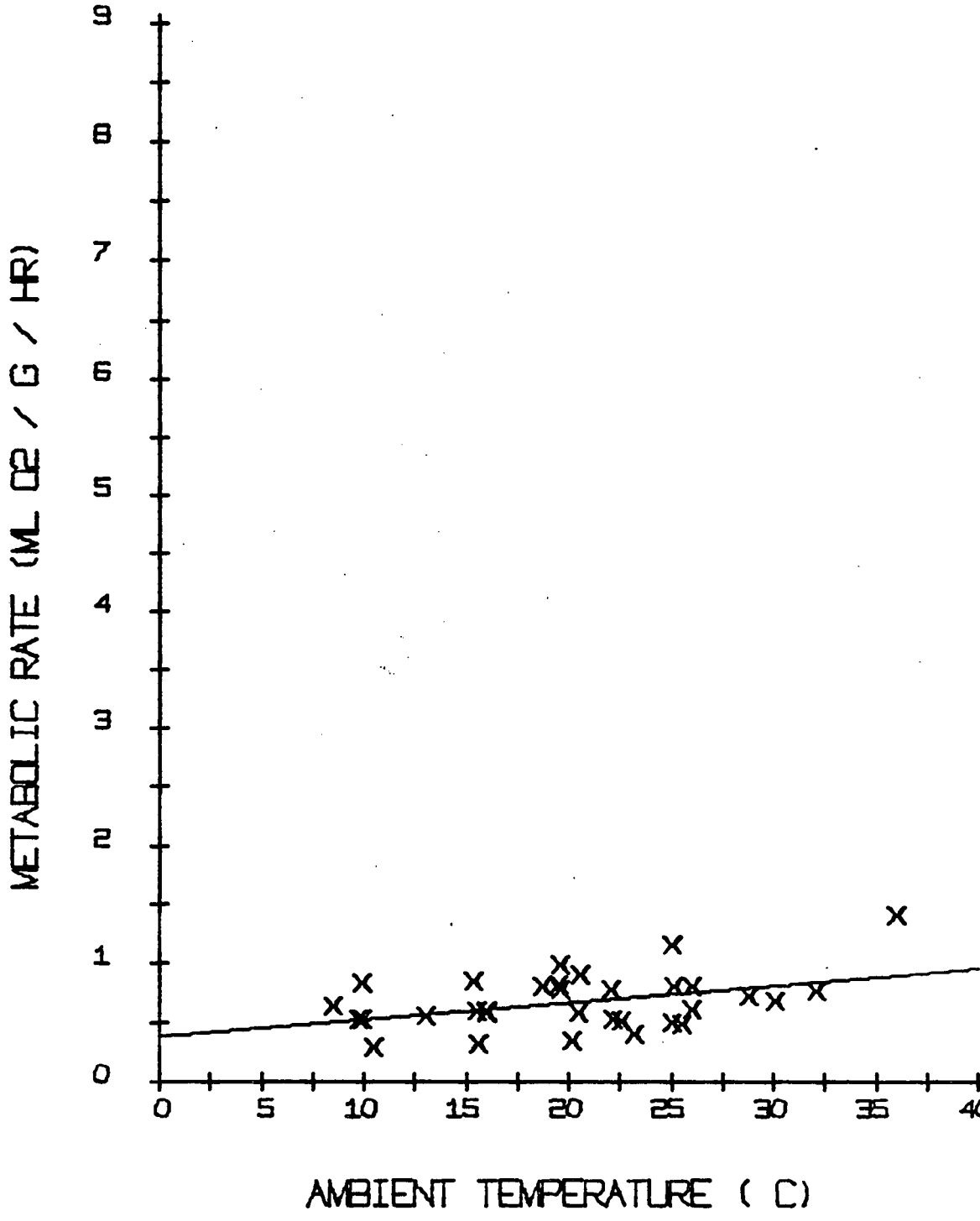
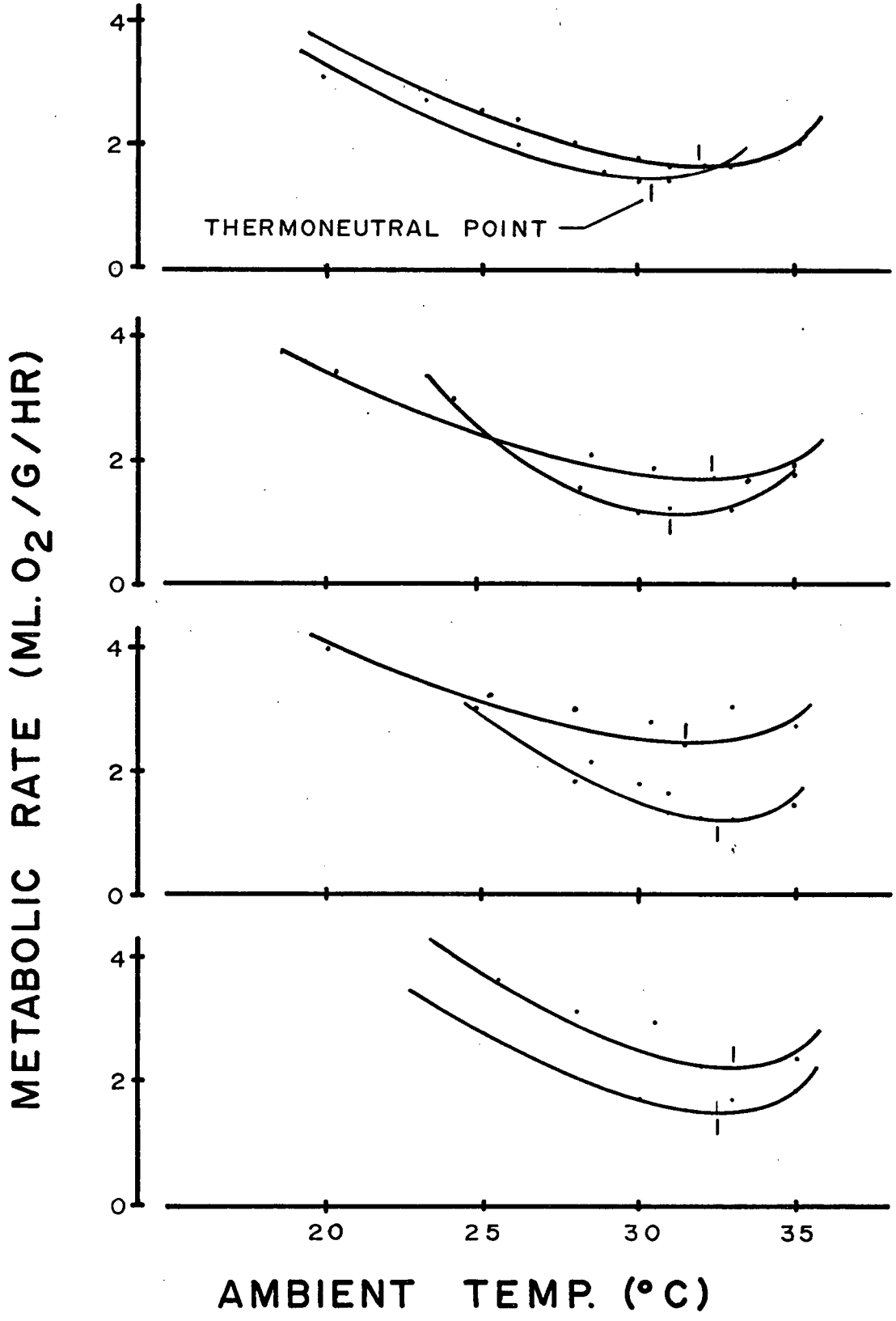


FIG. 3 THERMONEUTRAL ZONE

(EACH CURVE REPRESENTS ONE ANIMAL)



assume that they are true indicators of the biological situations.

To express metabolic rate in caloric terms, it is necessary to know the respiratory quotient (R.Q.). R.Q. is defined as the ratio of CO_2 produced to O_2 consumed. The R.Q. varies from 1.0 for carbohydrate metabolism to about 0.7 for fat metabolism. The caloric equivalent of oxygen corresponding to the various R.Q. values was obtained from Brody (1945). Fig. 4 shows a linear regression of R.Q. over a range of T_A for non-torpid animals, and Fig. 5 shows a similar curve for torpid animals. The probability of the slope being zero is 0.012 for non-torpid and 0.008 for torpid. Again, we may assume that these slopes have valid biological meaning. The shift to a lower R.Q. indicates a trend towards metabolism of lipids rather than carbohydrates or proteins.

Oxygen consumption during entry into torpor at 15 C (T_A) was measured at short intervals of time for three animals. These curves had a similar form. All animals required about 1.5 hr to reach the torpid state, and the area under the curve was approximately 35% of the corresponding area prior to entry (normothermic level). One such curve is shown in Fig. 6.

Oxygen consumption during arousal from torpor at 10 C (T_A) was measured before and after the onset of shivering. Before shivering, the mean M.R. (metabolic rate) and the S.D. (standard deviation) for a group of

FIG. 4

RELATIONSHIP OF RESPIRATORY QUOTIENT TO AMBIENT TEMPERATURE

Y = .6 3702 + .0 0269X N = 84

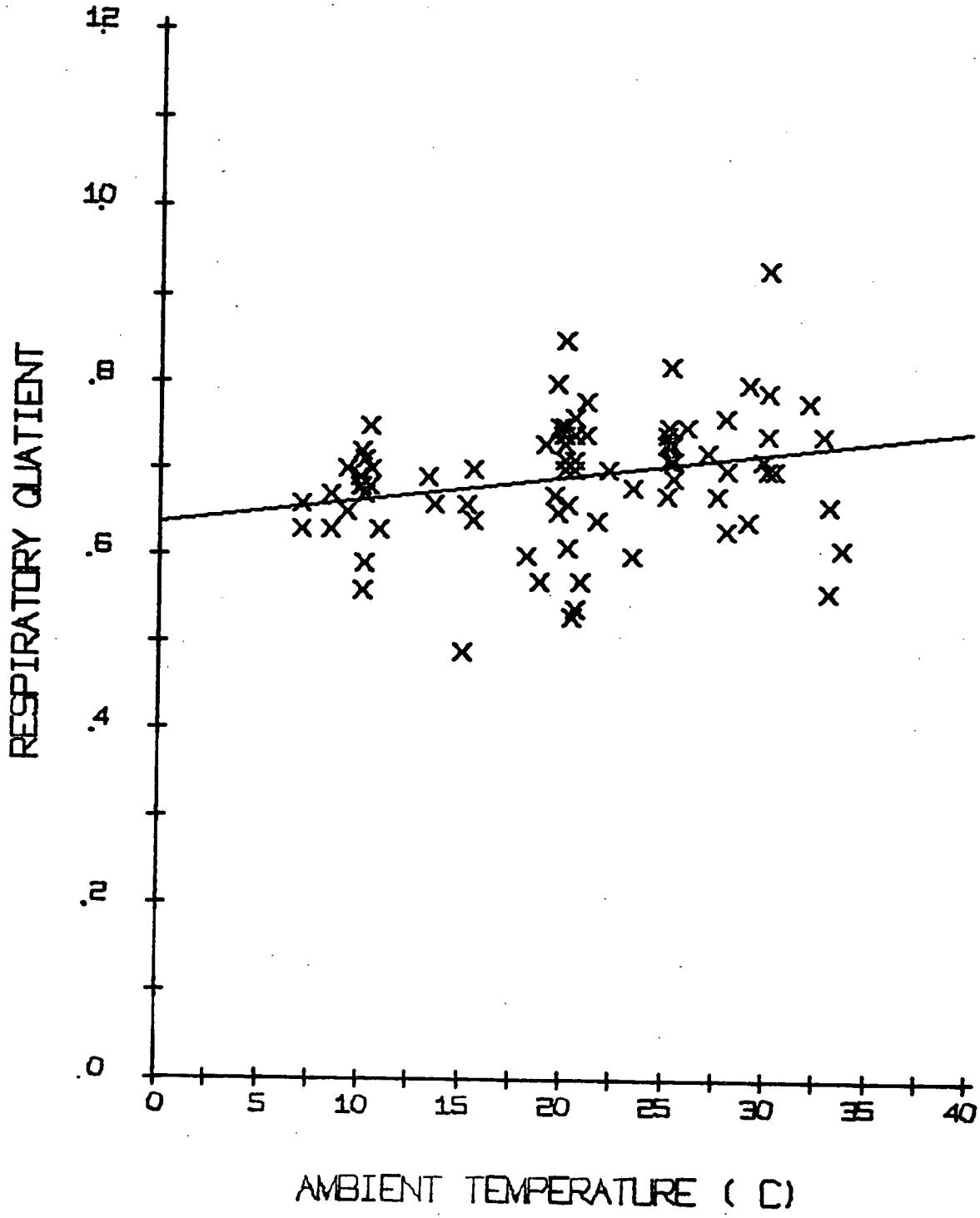


FIG. 5

RELATIONSHIP OF RESPIRATORY QUOTIENT OF TORPID ANIMALS TO AMBIENT TEMPERATURE

Y = .2 6074 + .0 2042X N = 20

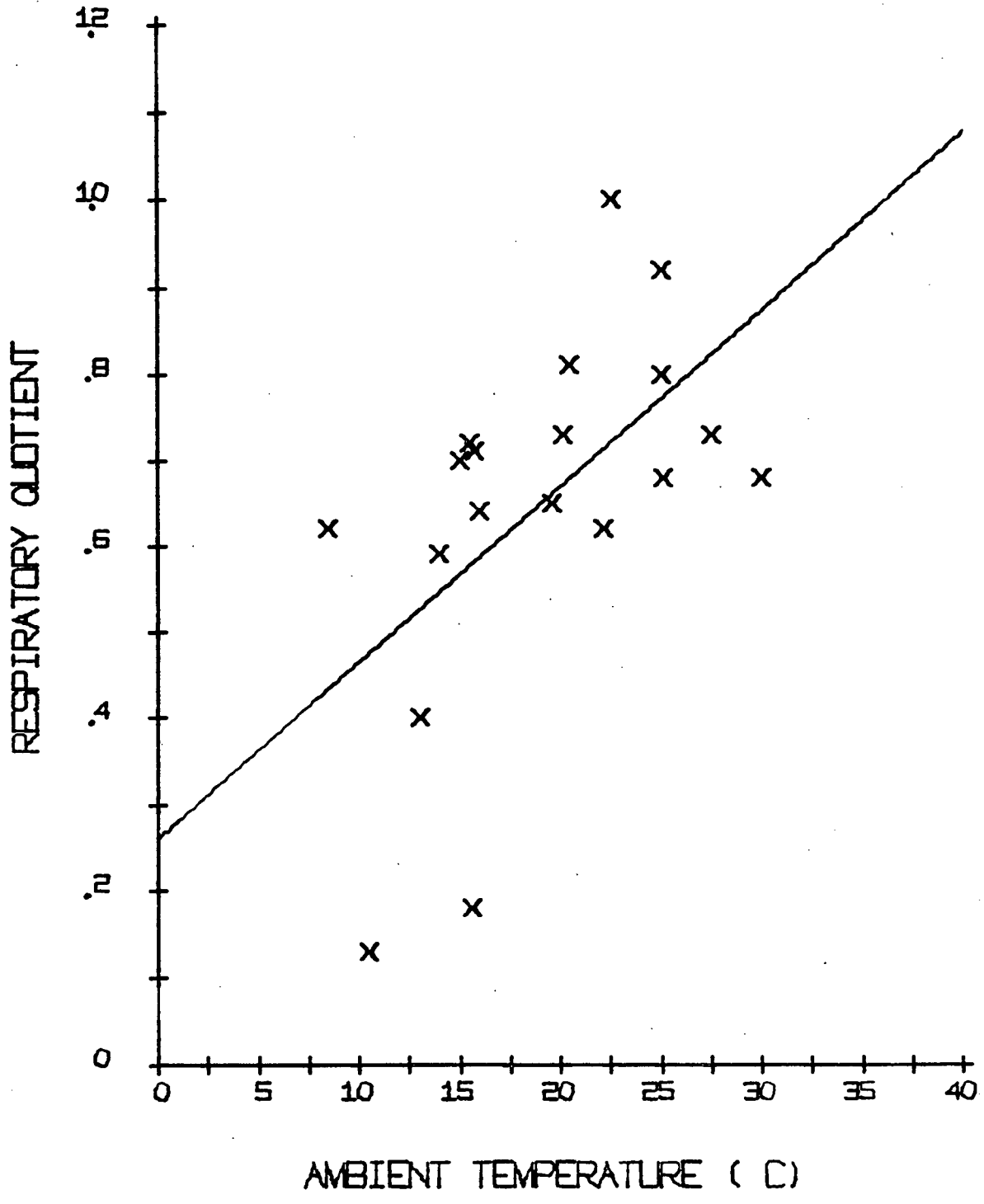
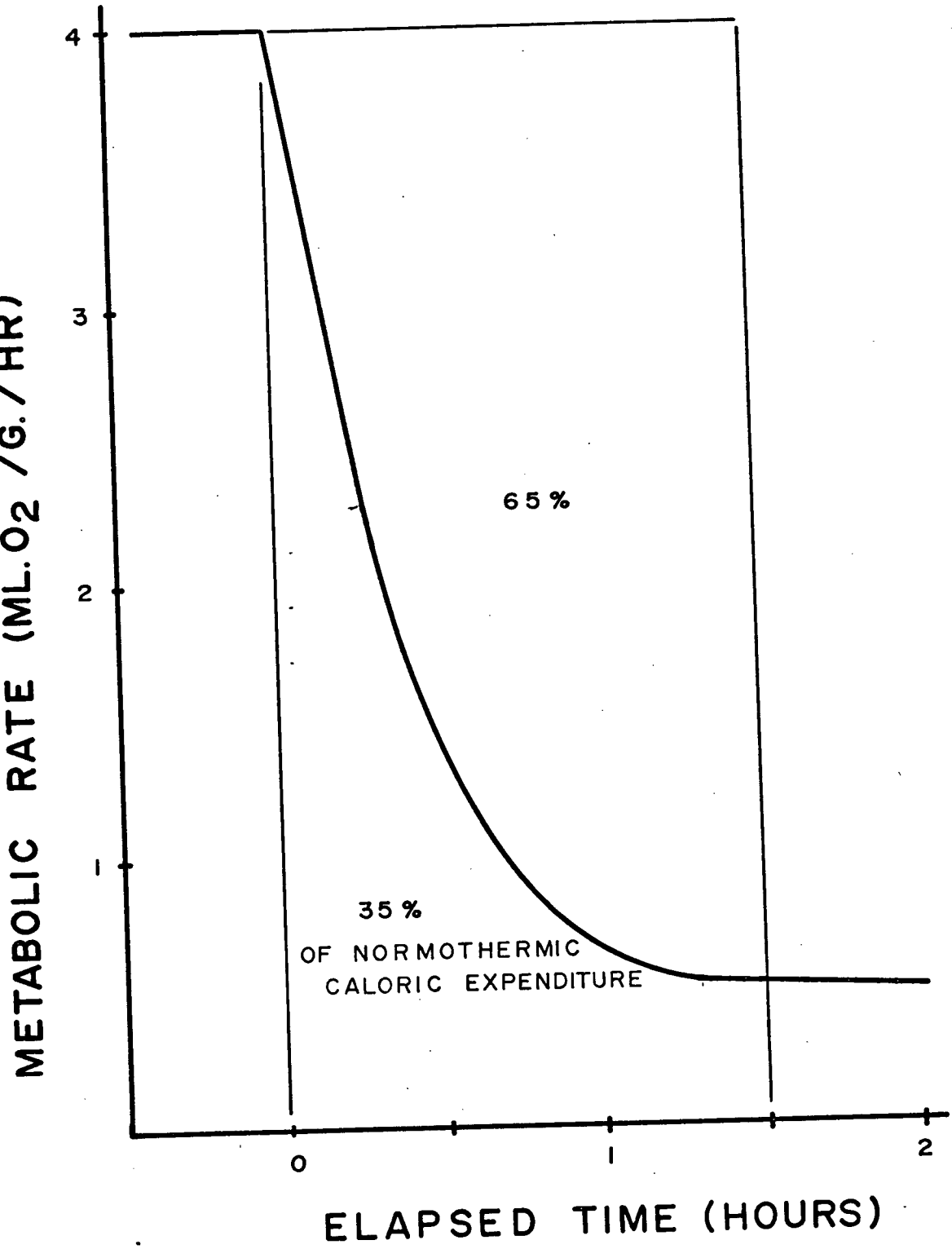


FIG. 6 CHANGE IN METABOLIC RATE DURING A TYPICAL ENTRY INTO TORPOR AT 15°C.



10 animals were 5.08 ± 0.77 ml O_2/g/hr. The R.Q. for this period was 0.51 ± 0.059. After shivering had commenced the mean M.R. and the S.D. were 7.28 ± 2.199, and the corresponding R.Q. values were 0.81 ± 0.151. These data are shown in Fig. 7. The shift in R.Q. from 0.51 to 0.81 may indicate a shift from lipid to carbohydrate substrate. Alternatively, it may indicate a release of CO_2 accumulated during torpor or a decrease in CO_2 fixation. The rate of increase of T_B (body temperature) was 0.53 C/min with a S.D. of 0.149. The mean total heat expended during arousal was 0.99 cal/g/C increase in T_B with a S.D. of 0.252.

Evaporative Water Loss

Evaporative water losses can occur from the skin or from the lungs. In both cases, one could expect the losses to be related to body weight at any given temperature, since both surface area and metabolic rate are functions of body weight. These evaporative water loss data have been plotted in three ways: mg water/hr, mg water/g body wt/hr, and mg water/ml O_2 consumed. The data for non-torpid animals appear in Figs. 8, 9, and 10, and the corresponding data for torpid animals are shown in Figs. 11, 12, and 13. The best fit of the data from normothermic animals was obtained when plotted as mg/ml O_2, indicating that pulmonary loss is the main component of water loss. However, the data from torpid animals had best fit when plotted as mg/hr, indicating that pulmonary loss was not dominant over cutaneous loss.

FIG. 7 METABOLIC RATES AND RESPIRATORY QUOTIENTS DURING AROUSAL AT 10° C.

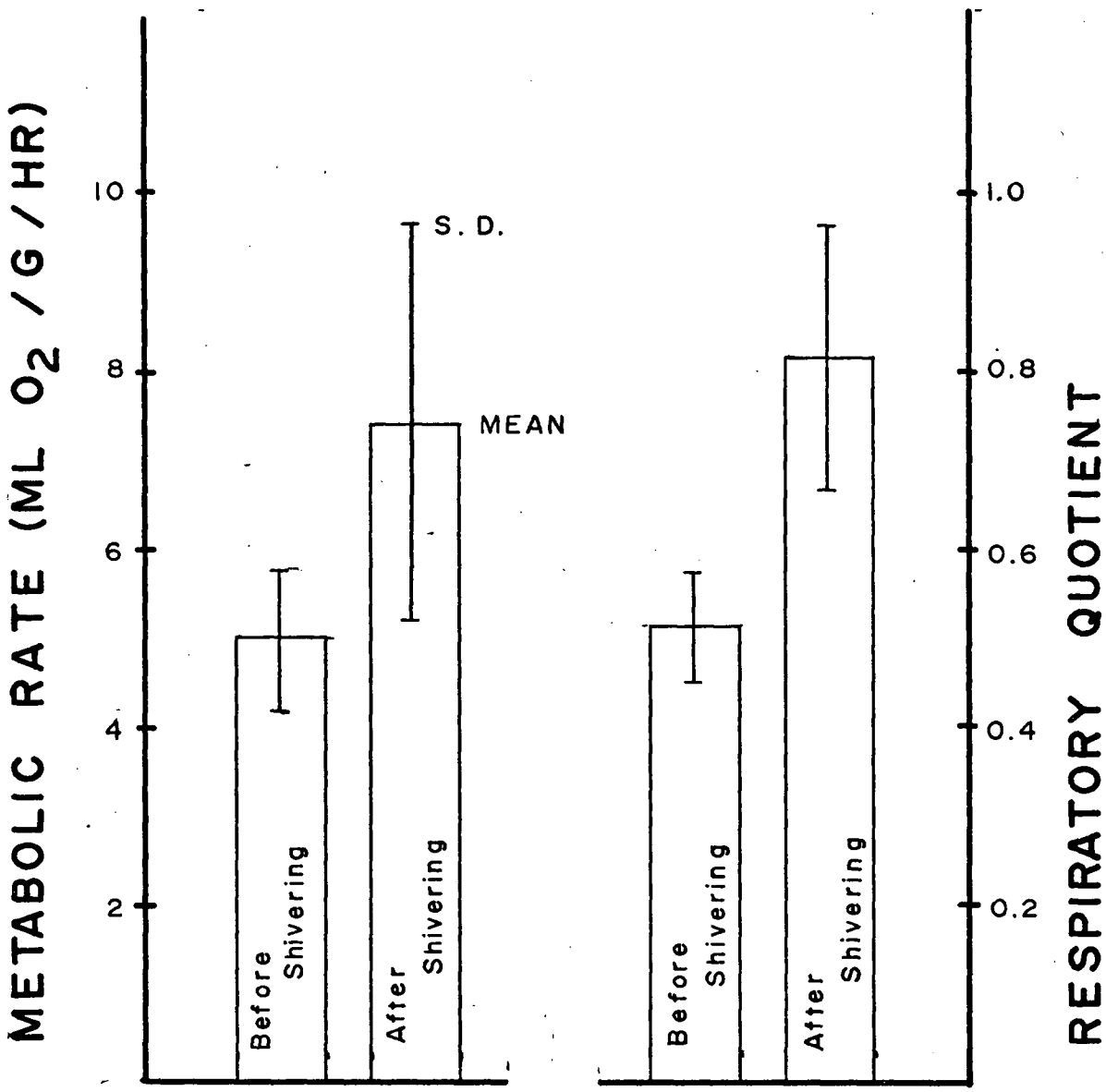


FIG. 8

RELATIONSHIP OF PULMO-CUTANEOUS WATER LOSS OF NON-TORPID ANIMALS TO AMBIENT TEMPERATURE

Y = 40.2818 + -0.1556X N = 56

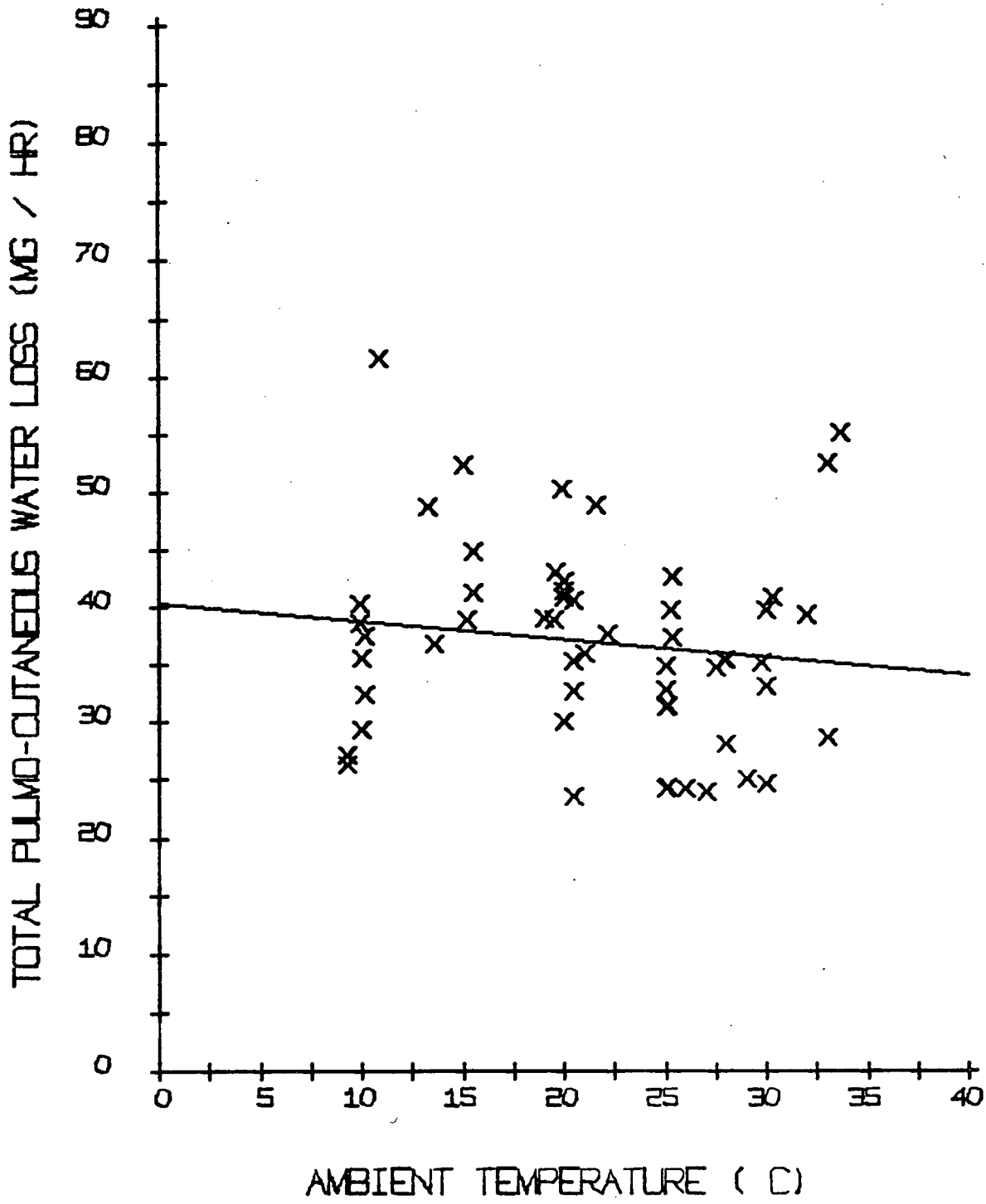


FIG. 9

RELATIONSHIP OF PULMO-CUTANEOUS WATER LOSS OF NON-TORPID ANIMALS TO AMBIENT TEMPERATURE

Y = 2.4283 + -0.0099X N = 56

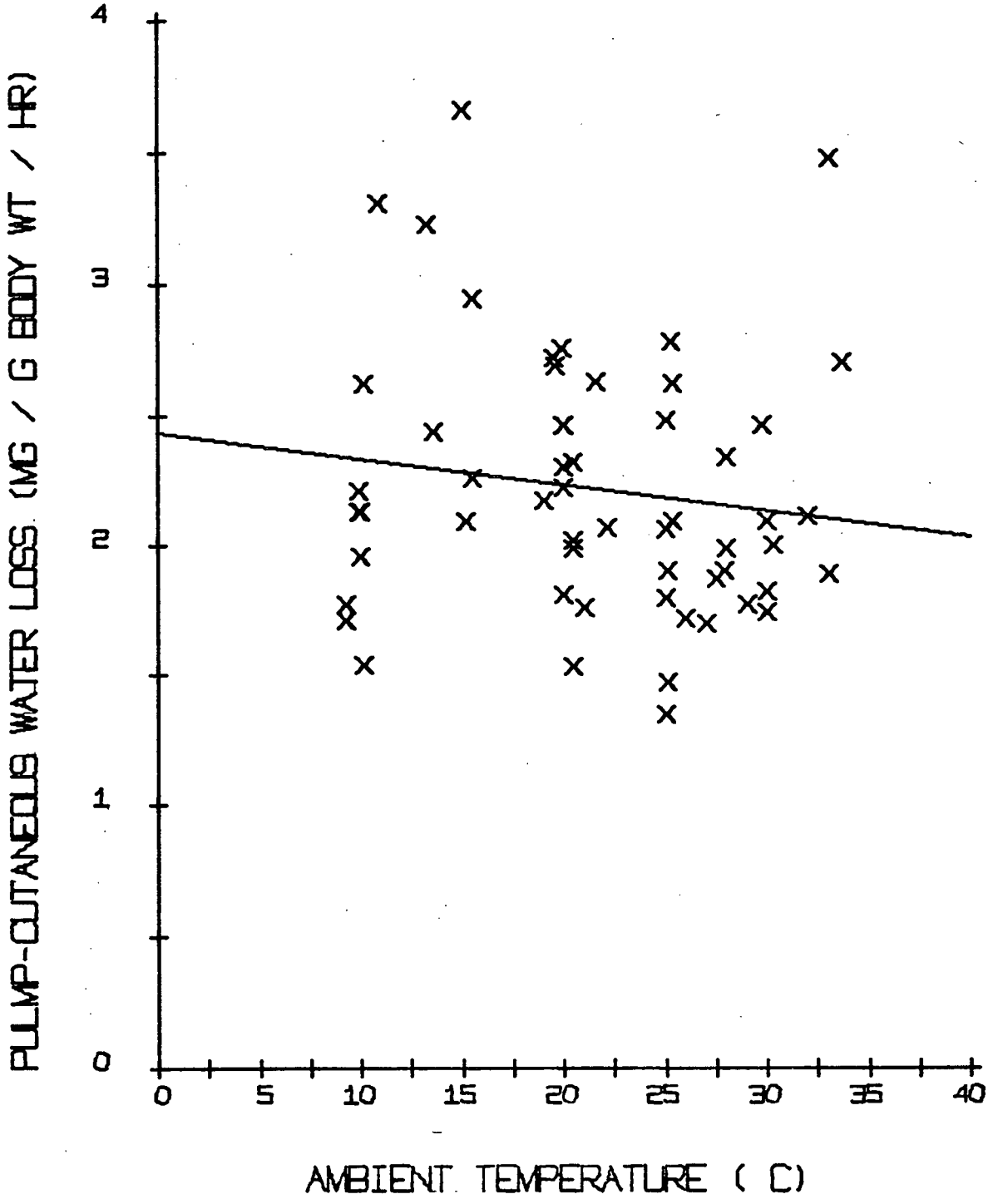


FIG. 10

RELATIONSHIP OF RELATIVE PULMO-CUTANEOUS WATER LOSS OF NON-TORPID ANIMALS TO AMBIENT TEMPERATURE

Y = -0.1006 + 0.0389X N = 56

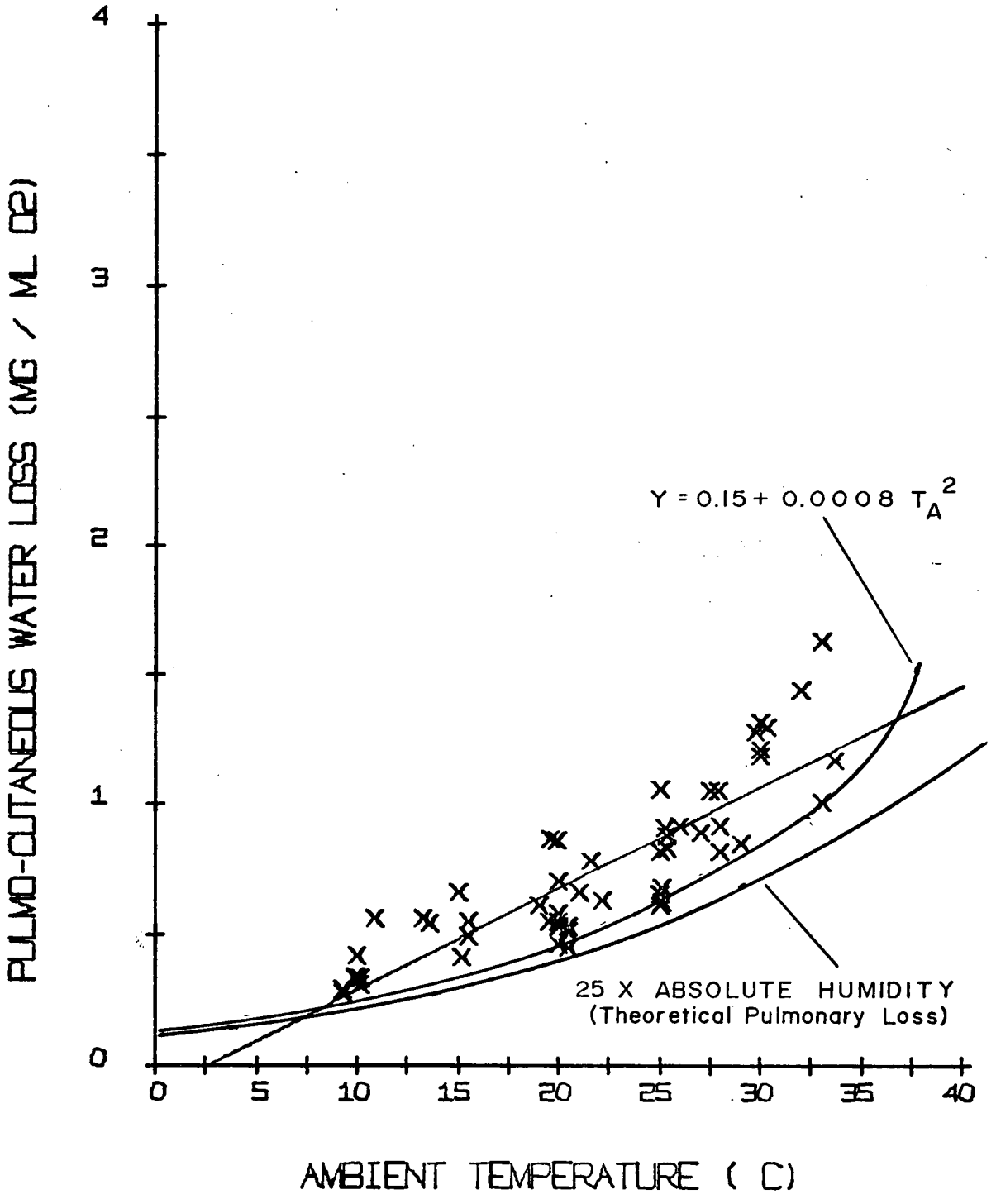


FIG. 11

RELATIONSHIP OF PULMO-CUTANEOUS WATER LOSS OF TORPID ANIMALS TO AMBIENT TEMPERATURE

Y = 14.4909 + 0.2540X N = 12

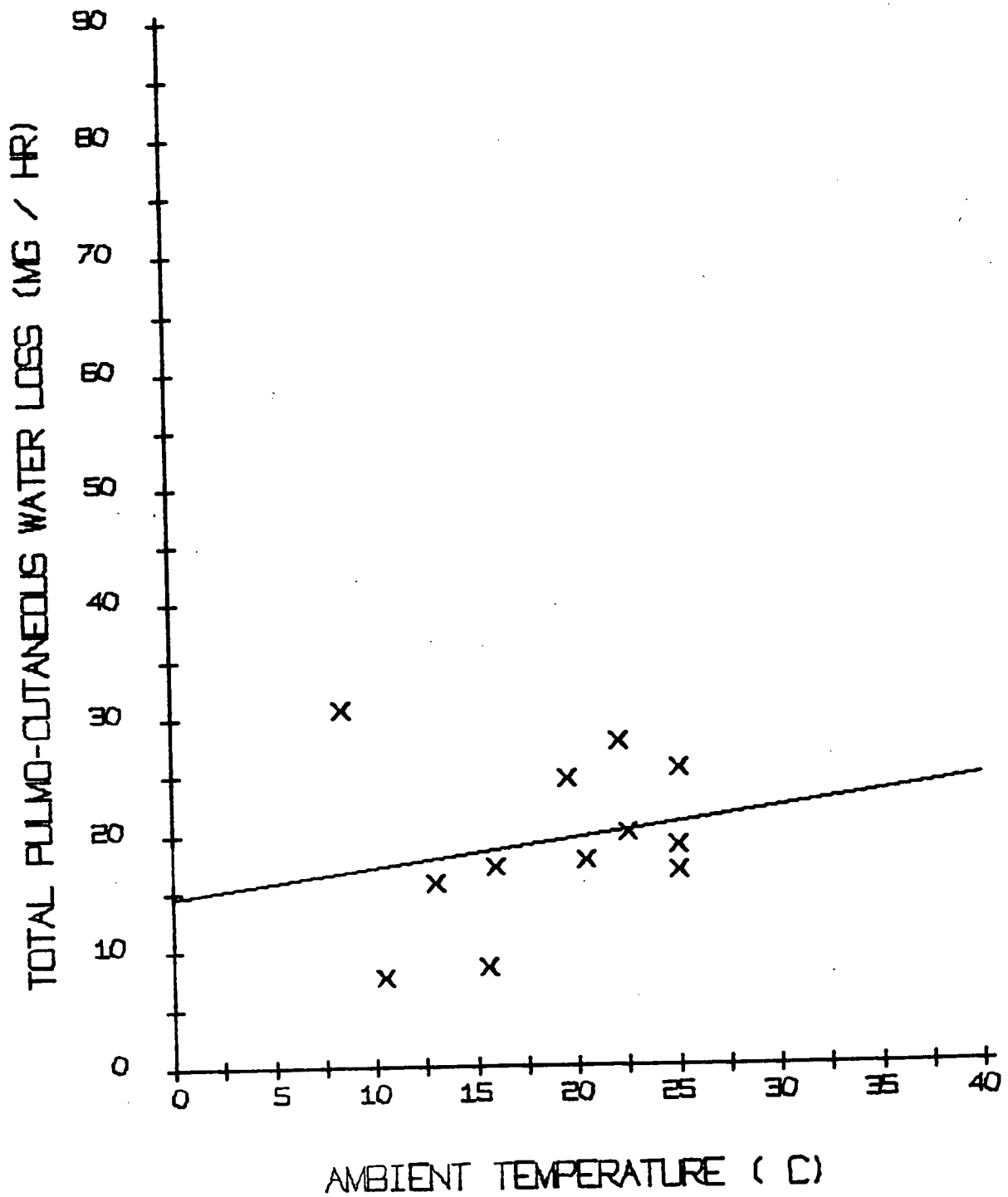


FIG. 12

RELATIONSHIP OF PULMO-CUTANEOUS WATER LOSS OF TORPID ANIMALS TO AMBIENT TEMPERATURE

Y = 1·1341 + 0·0042X N = 12

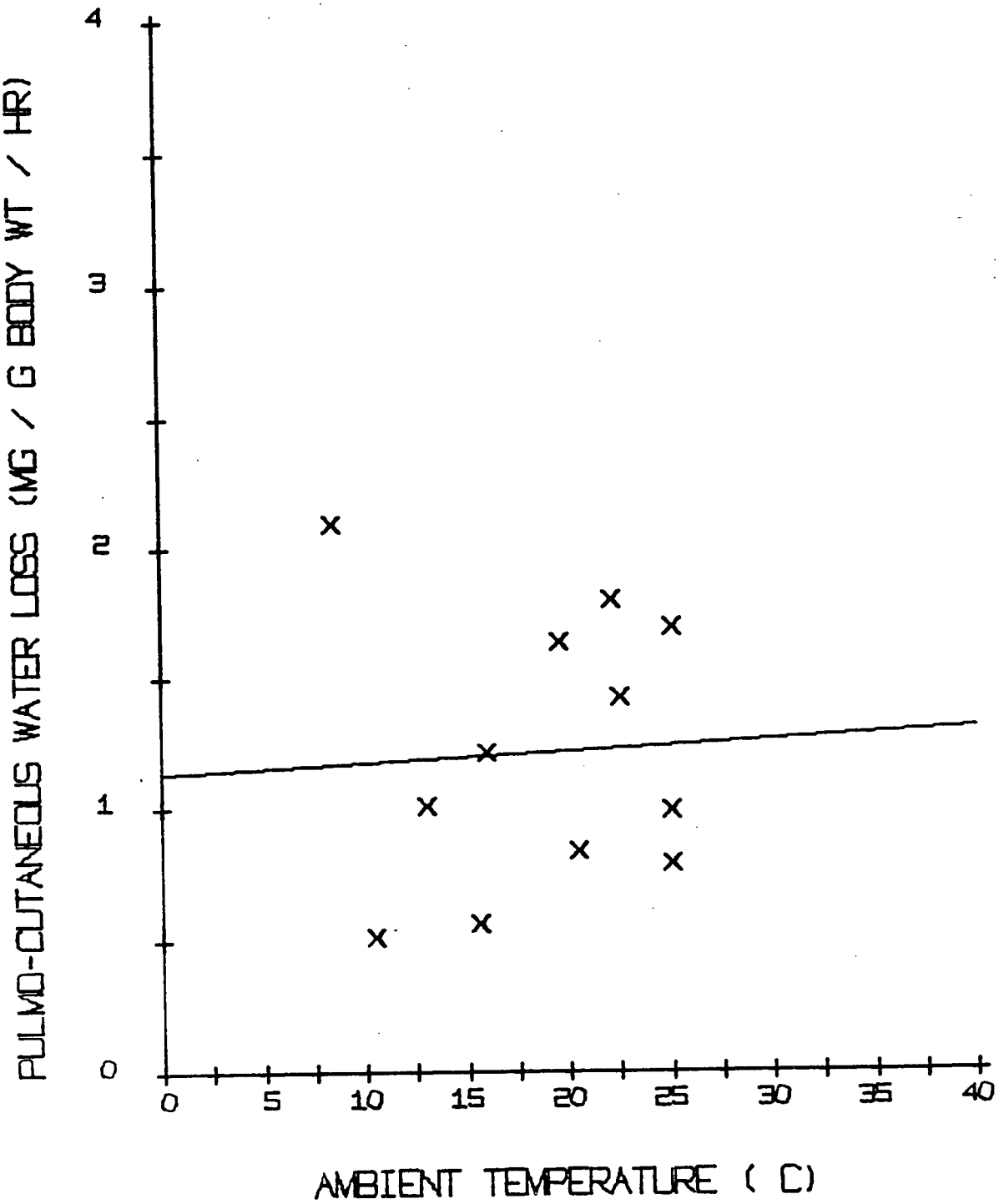
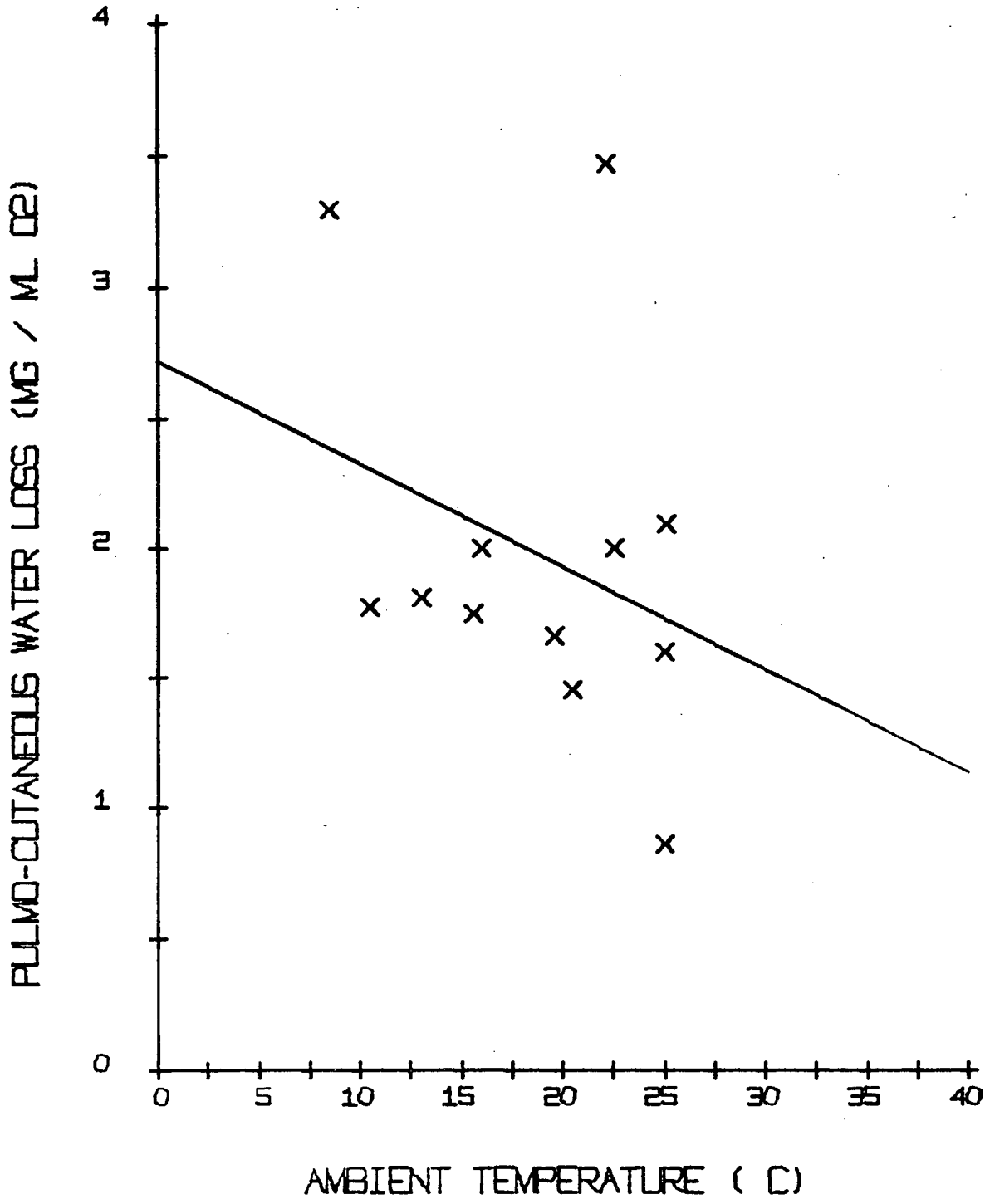


FIG. 13

RELATIONSHIP OF RELATIVE PULMO-CUTANEOUS WATER LOSS OF TORPID ANIMALS TO AMBIENT TEMPERATURE

Y = 2.7208 + -0.0397X N = 12



The ratio of "pulmonary + head skin" loss: "body skin" loss, will be referred to as Pulmonary: Cutaneous loss ratio. These ratios ranged from 65:35 to 79:21, with both mean and mode of 72:28. The cutaneous loss ranged from 6.1 mg/hr to 20.0 mg/hr. The tranquilizer did not appear to affect the pulmonary or cutaneous components of water loss, since total evaporative loss remained essentially the same as for normal animals. The only noticeable effect was a very slight depression of metabolic rate.

Cutaneous water loss, as determined on dead animals, varied from 6.0 mg/hr to 30.0 mg/hr. These data are shown in Fig. 14. Surface area varied with body weight as shown in the double-logrithmic plot in Fig. 15. The relationship of body surface to body weight is $A = 20.25\ W^{0.38}$, where area (A) is in square centimeters and body weight (W) is in grams. The water loss data from this experiment are in agreement with the estimates of cutaneous water loss of live animals from the previous experiment.

FIG. 14

RELATIONSHIP OF CUTANEOUS WATER LOSS OF DEAD ANIMALS TO AMBIENT TEMPERATURE

LOG Y = 0·8964 + 0·0120 X N=30

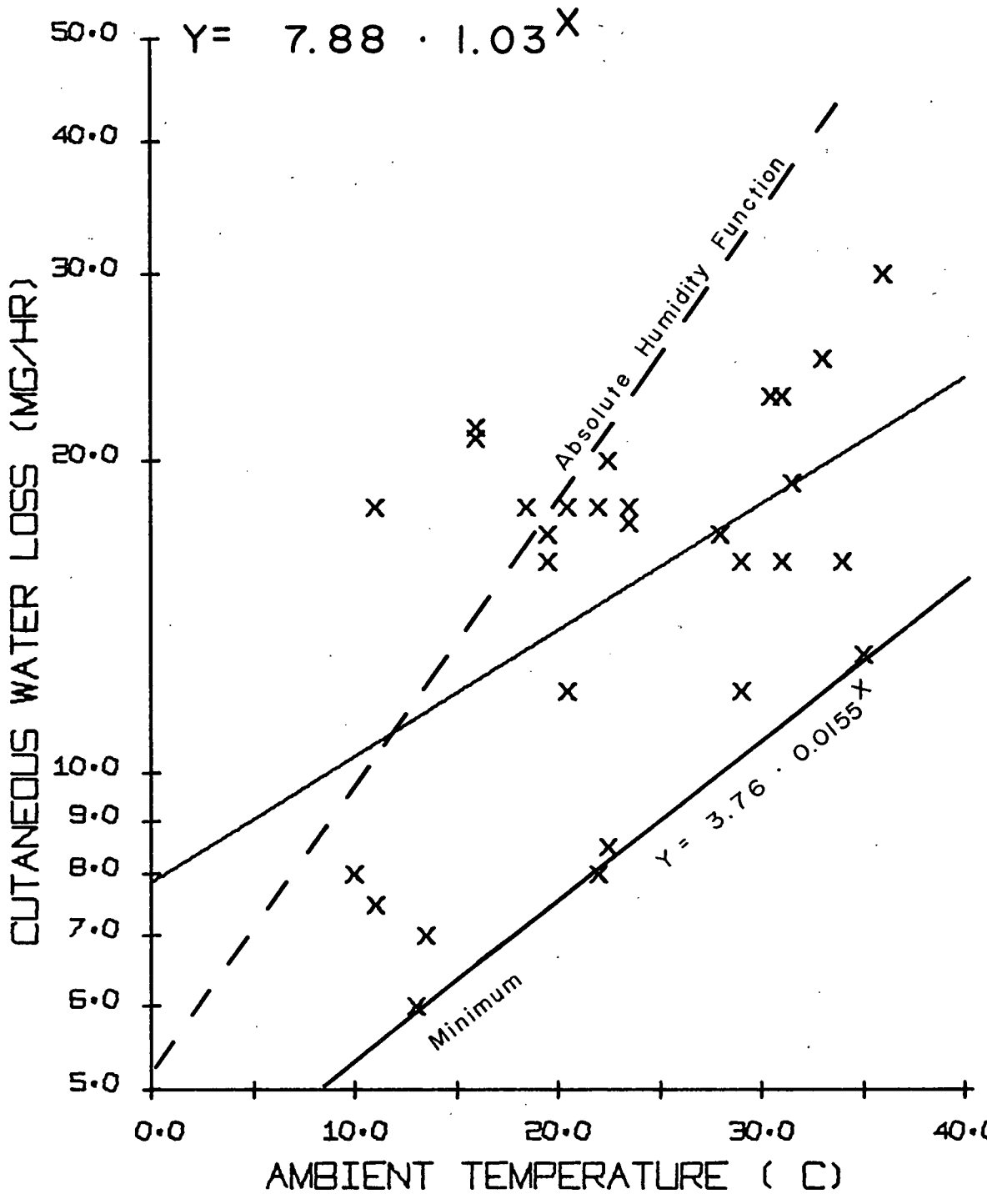
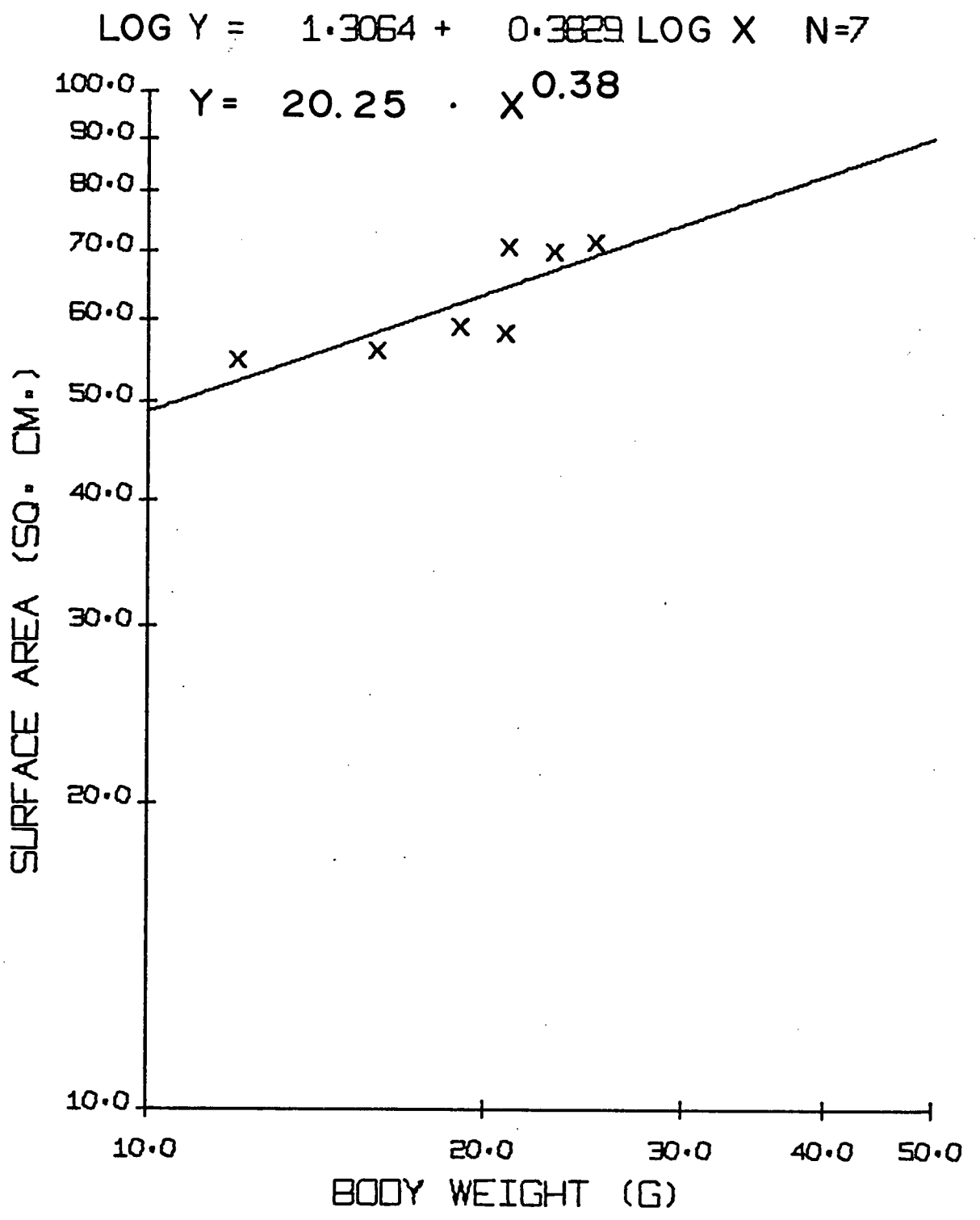


FIG. 15

RELATIONSHIP OF BODY SURFACE AREA TO BODY WEIGHT



DISCUSSION

Energy Requirements

The data obtained in this study can be compared with data on similar species by using the "basal" metabolic rate and the slope of the metabolic rate curve as standards of comparison. The slope of the metabolic rate curve can be taken as a measure of the rate of heat loss, and it is referred to as conductance (C). The data from this study yield a basal M.R. of 1.75 ml O_2/g body wt/hr (12.25 cal/g/hr) and a conductance of 0.24 ml O_2/g/hr/C (1.128 cal/g/hr/C). The average body weight was 17.0 g. These metabolic values are, of course, averages from a family of curves. The BMR and Conductance can be expected to vary with body weight, insulation, season, and surface area.

A number of workers have contributed to our knowledge of energetics of the heteromyids. Dawson (1955) gives a conductance = 0.176 and BMR = 1.2 for the kangaroo rat Dipodomys merriami (average weight = 35 g) and similar values of 0.158 and 1.2 for the larger D. panamintinus (average weight = 60 g). Bartholomew and MacMillen (1961) reported data for the kangaroo mouse, Microdipodops pallidus, (wt = 15 g) indicating a BMR of 1.3 ml/g/hr and a conductance of about 0.1 ml/g/hr/C. However, higher values (BMR = 1.8 and conductance = 0.185) for the same species were reported recently by Brown and Bartholomew (1969). It is likely that the low values in the earlier work were the result of a tendency for

the animals to become hypothermic at low ambient temperatures. Tucker (1965 a) provides a basal rate of 0.97 and a conductance of 0.18 for Perognathus californicus (wt = 22 g). Values for P. hispidus (wt = 40 g) are 1.25 and 0.201 (Wang and Hudson, 1970).

Brody (1945) and Kleiber (1961) have produced equations, based on large numbers of species, that relate BMR to body weight. Herreid and Kessel (1967) have developed a similar equation to relate conductance to body weight. It is interesting to compare the data from this study and data from other small nocturnal, fossorial rodents to these theoretical curves. Fig. 16 shows the comparisons for BMR, and Fig. 17 shows the comparisons for conductance.

Although the data from this study are in agreement with the theoretical predictions for a 17 g mammal, most other desert-adapted rodents have a lower BMR than predicted. Hayward (1964) suggests that the tendency for heteromyids to store fat, a tissue that has a low metabolic rate, could be responsible for the lower BMR values reported for that family of rodents. This would be consistent with the higher BMR for P. parvus reported here, since very few of the animals used in this study appeared to have large stores of fat. Schreiber (pers. comm.) examined P. parvus throughout the year and found that the fat content was less than 0.8 g, or about 5% of the fat-free body weight. Another

FIG. 16

RELATIONSHIP OF BMR OF FOSSORIAL RODENTS TO BODY WEIGHT

LOG Y = 0.6656 + -0.3628 LOG X N=20

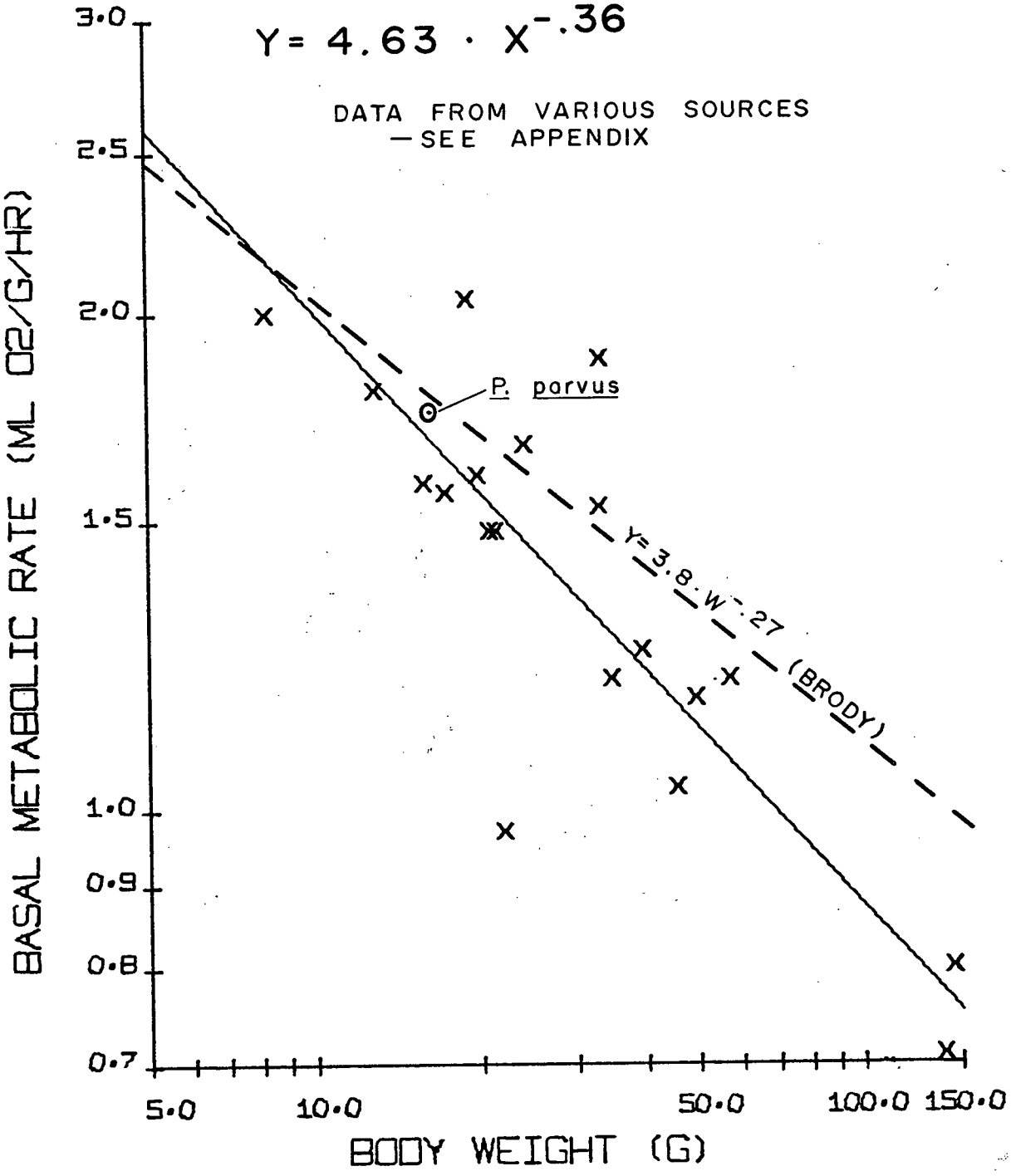
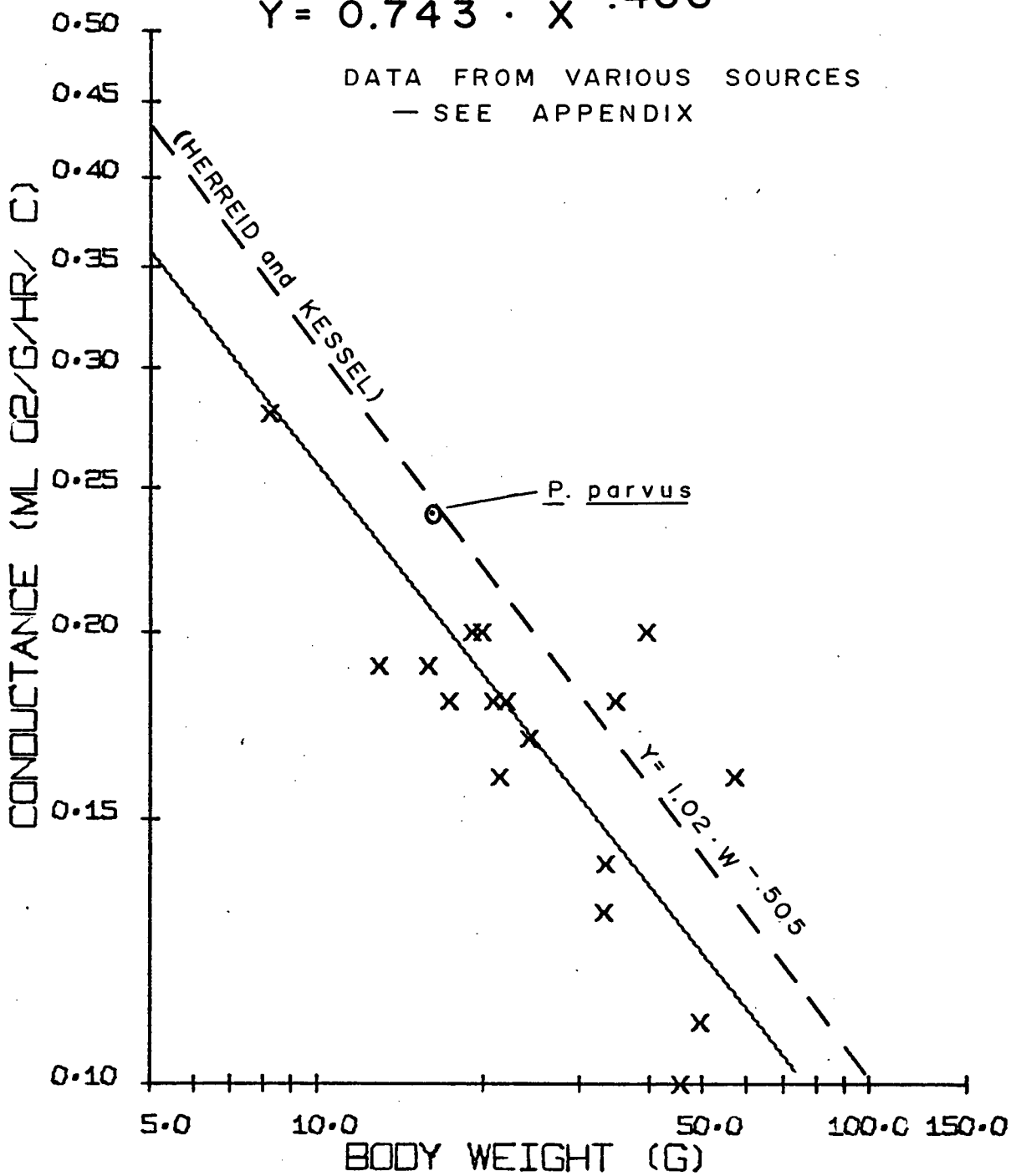


FIG. 17

RELATIONSHIP OF CONDUCTANCE OF FOSSORIAL RODENTS TO BODY WEIGHT

LOG Y = -0.1291 + -0.4664 LOG X N=20

$Y = 0.743 \cdot X^{-.466}$



possible explanation for lowered BMR's in desert rodents can be extracted from recent findings (Schmidt-Nielsen et al., 1970) that the counter-current heat exchange mechanism in the kangaroo rat permits the saving of 8.8% to 16.1% of the heat produced. This, of course, does not help to explain the higher values for P. parvus, since its counter-current heat exchange seems to be about as efficient as that of the kangaroo rat. It is possible that slight differences in body form, such as a smaller head size, with concomitant changes in surface:volume ratio combine with lower fat levels to produce the higher BMR for P. parvus. It is interesting to note that the BMR for Peromyscus maniculatus from the same area as P. parvus is 1.99 ml/g/hr (Hayward, 1964). These two species are almost identical in size and body form, and they are sympatric in some areas. The similarity in their metabolic parameters suggests that the higher BMR has some adaptive value in the northern part of the range, or that fat storage is of less value. Hayward (1964) found that P. maniculatus from a southern desert habitat had a greater tendency to store fat than the animals from the Okanagan Valley. Although it is not possible to provide a definitive answer to the question of why heteromyids in particular, and desert rodents in general, have lower BMR's than predicted by Brody's equation, it seems very likely that P. parvus does fit the theoretical predictions for BMR and conductance. It would be

interesting to measure BMR, conductance, fat levels, and body surface areas of field specimens of all species in the family Heteromyidae.

The data for normothermic animals (Fig. 1) show large variation. I have not calculated confidence limits for this metabolic rate curve, since no statistical comparisons are made with other curves. However, it is necessary to determine the source of the variation. Plots of metabolic rate over body weight at T_A's of 10, 20, and 30 C are shown in Figs. 18, 19, and 20. Definite body weight effects are indicated at 10 and at 30 C, but the slope of the curve at 20 C is not significantly different from zero at the 5% level of confidence. These body weight effects have contributed to the variability of the data. Additional variability probably has been introduced by seasonal changes in the animals, since data were collected throughout the year. Thus, the range of values shown in Fig. 1 is representative of the total variation one could expect to encounter in this species.

The respiratory quotient for normothermic animals has a tendency to increase with increasing T_A. The average R.Q. for these data is 0.72, corresponding to the R.Q. for fat metabolism. Since the animals were on a high-fat diet of sunflower seeds and were post-absorptive, these values are normal. The R.Q. of 0.72 corresponds to a caloric equivalent of oxygen of 4.7 cal/l (Brody, 1945), and this value was used in converting oxygen consumption to calories.

FIG. 18

RELATIONSHIP OF METABOLIC RATE TO BODY WEIGHT AT 10 C

Y = 12.6481 + -0.3676X N = 13

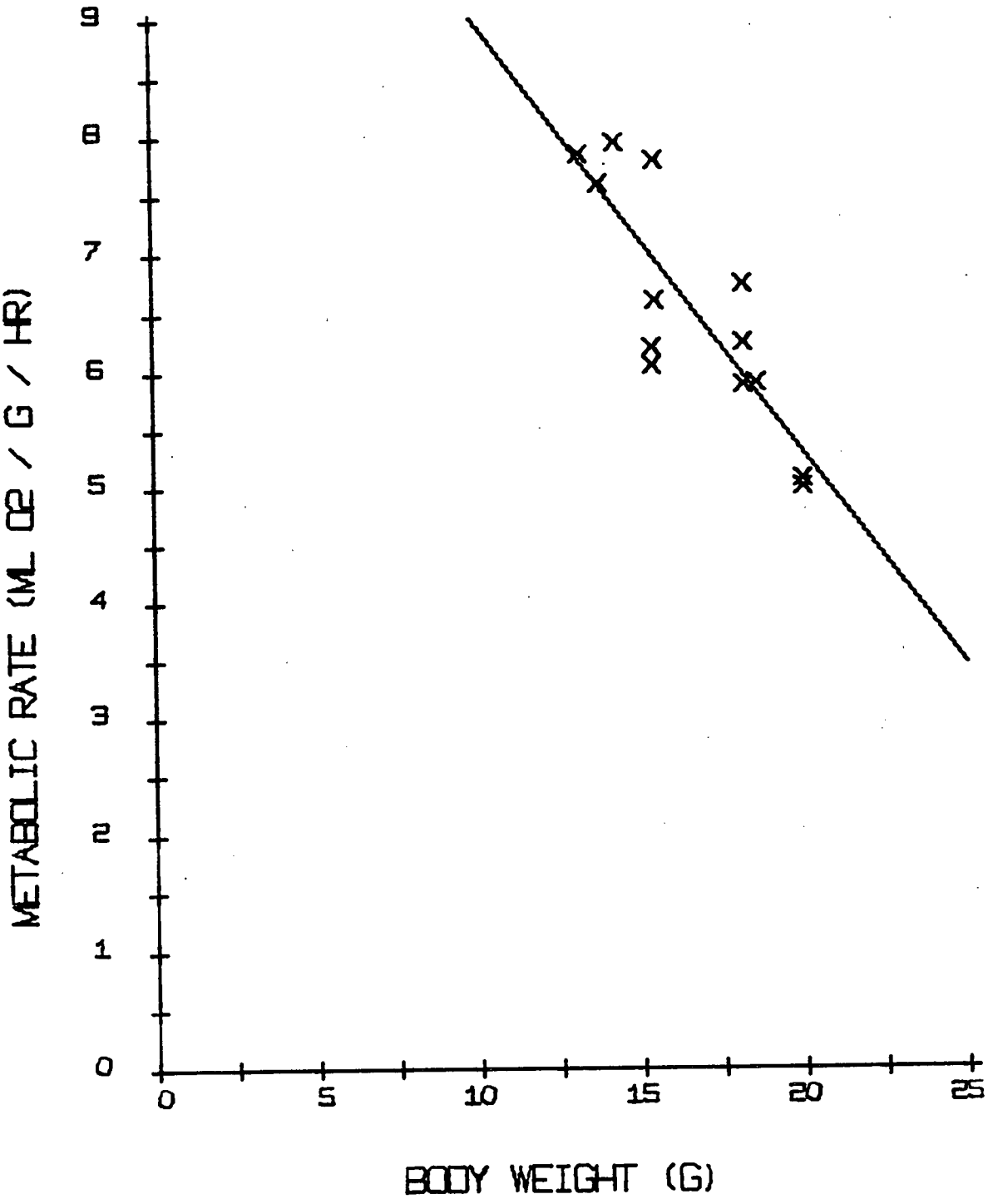


FIG. 19

RELATIONSHIP OF METABOLIC RATE TO BODY WEIGHT AT 20 C

Y = 5.6792 + -0.1232X N = 27

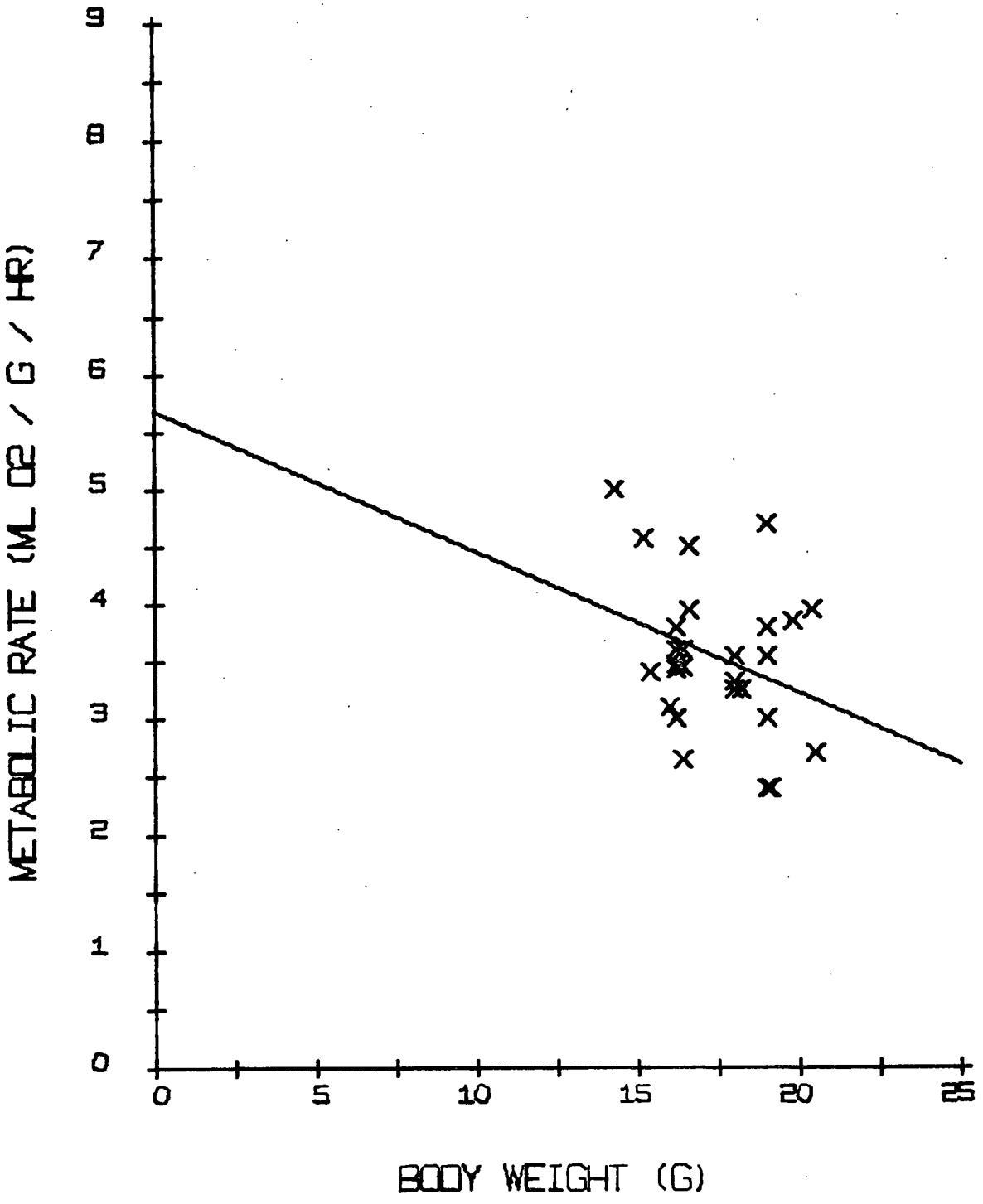
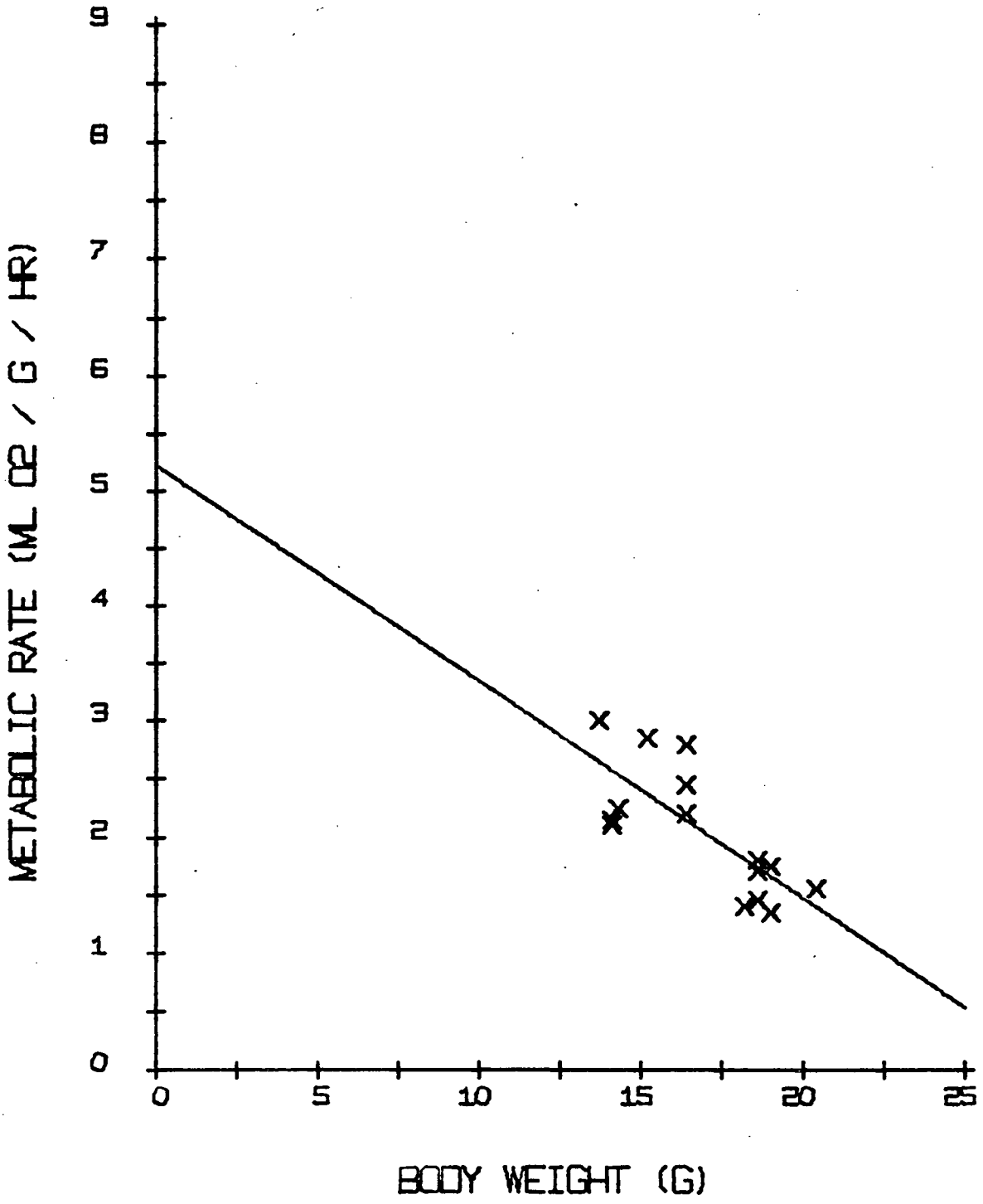


FIG. 20

RELATIONSHIP OF METABOLIC RATE TO BODY WEIGHT AT 30 C

Y = 5.2215 + -0.1878X N = 15



1. Torpor

P. parvus, like most heteromyids, has the ability to abandon homeothermy for the heterothermic state. Characteristically, the body temperature will be 1 - 2 C above the ambient temperature. Obviously, this reduction in body temperature is accompanied by a depression of metabolic rate. Fig. 2 shows that the metabolic rate during torpor is a positive function of ambient temperature, the slope of the curve being 0.0144. Lasiewski (1963) observed a M.R. of 0.2 ml/g/hr in torpid hummingbirds at 16 C. The slope of the curve for hummingbirds appears to be approximately 0.03. The general shape of the curve for hummingbirds is quite similar to the corresponding curve for P. parvus. Chew et al. (1967) report a minimum O_2 consumption for torpid P. longimembris as follows:

$$ml/g/hr = -0.177 + 0.027\ T_A \qquad T_A \text{ below } 22\ C$$

$$ml/g/hr = -0.68 + 0.048\ T_A \qquad T_A \text{ above } 22\ C$$

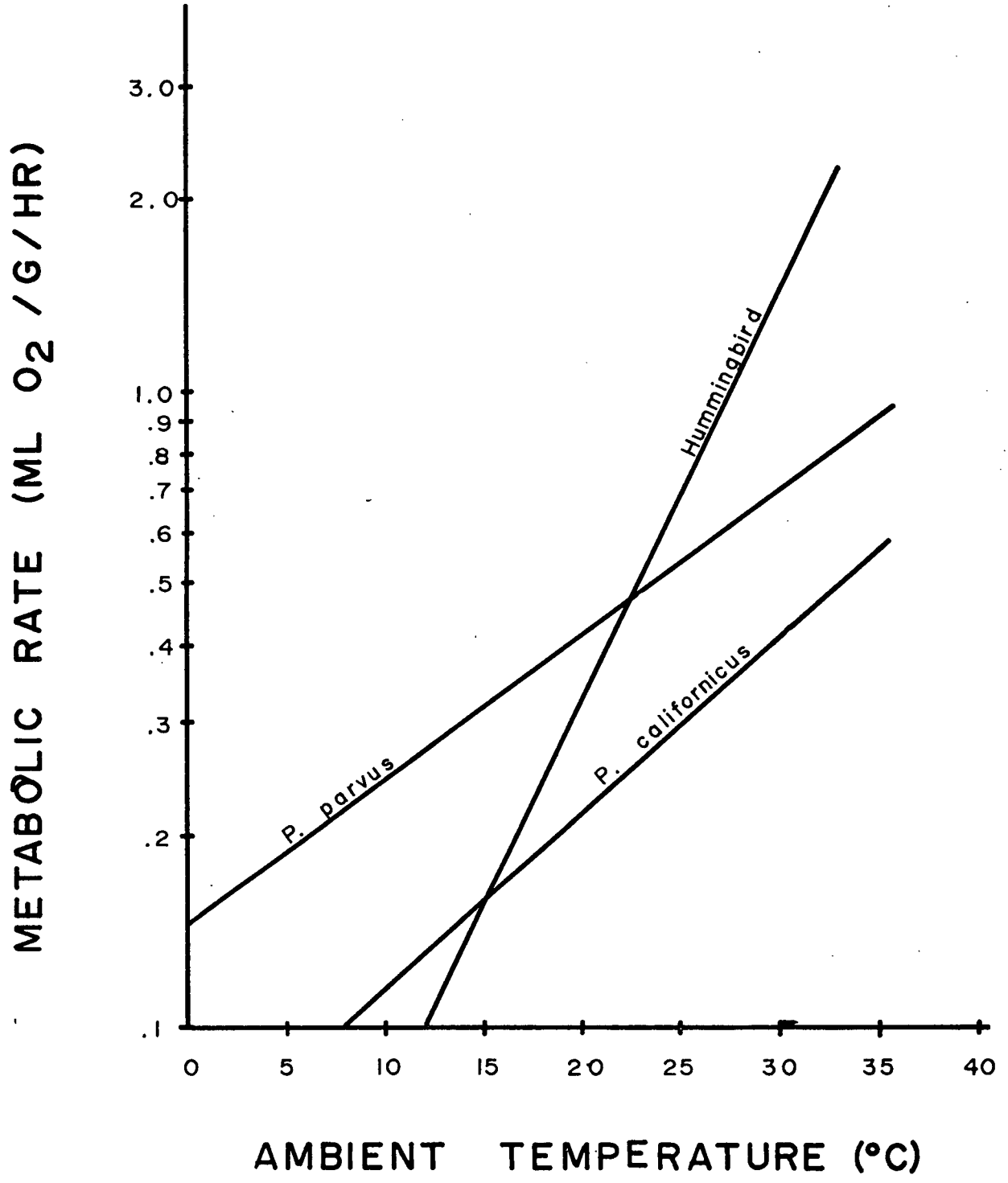
Tucker (1965) has provided similar curves for torpid P. californicus:

$$ml/g/hr = 0.04 + 0.008\ T_B \qquad \text{below } 21\ C$$

$$ml/g/hr = -0.74 + 0.045\ T_B \qquad \text{above } 21\ C$$

If a smooth curve is drawn through the minimum values shown for P. californicus, and the curve re-plotted on a semi-logrithmic scale as Lasiewski (1963) has done for torpid hummingbirds, the result is a straight line. Fig. 21 compares my data for torpid P. parvus with the

FIG. 21 MINIMUM METABOLIC RATES IN TORPOR



curve for torpid P. californicus and the curve for torpid hummingbirds. The curves for the two species of Perognathus have similar slopes, and the slopes are much less than the slope of the hummingbird curve. The approximate Q_{10} values for these curves, calculated for the interval of 20 - 30 C are: Hummingbird = 5.0, P. parvus = 1.7, and P. californicus = 1.8. Thus, the metabolism of the hummingbird is much more responsive to temperature than are the two species of Perognathus. Since chemical reaction rates are usually more than doubled by an increase of 10 C (Q_{10} greater than 2.0), it is possible that Perognathus regulates body temperature to some extent while in the torpid condition. Without data for more species, we cannot be sure that the similarity between the curves for Perognathus is not merely fortuitous. A comparative study of energetics of torpor in the heteromyids would be a welcome addition to the literature.

2. Entry into torpor

Very few data were collected on metabolic rate during the entry phase of the torpor cycle, but the curve shown in Fig. 6 seems to be representative of the minimum M.R. during entry. As pointed out previously, this type of entry requires approximately 1.5 hr, and the area under the curve represents about 35% of the normal homeothermic caloric expenditure. P. californicus appears to require 1.5 - 2.0 hr to

enter torpor (Tucker, 1965), and the general shape of the curves for body temperature and oxygen consumption are comparable to the curve in Fig. 6. Chew et al. (1967) indicate that about 1.5 hr are required by P. longimembris for entry into torpor at 10 C. Thus, P. parvus enters torpor in a manner that is essentially identical with that of the other pocket mice that have been studied.

3. Arousal from torpor

Arousal occurs in two relatively distinct stages, a non-shivering stage and a shivering stage. Data for P. longimembris (Bartholomew and Cade, 1957), P. californicus (Tucker, 1965), and P. hispidus (Wang and Hudson, 1970) indicate that shivering begins after body temperature has risen to 20 C. Shivering did not appear, or was not intense, below 20 C (T_B) in these species. Since chronically implanted thermistors were not used in this study, it was not possible to obtain simultaneous measurement of oxygen consumption and body temperature. Thus, the rates of arousal are average rates of increase of body temperature over both stages of arousal. These rates of increase in T_B varied from 0.21 to 0.71 C/min. The average rate was 0.53 C/min. Bartholomew and Cade (1957) report an arousal rate of about 0.60 C/min for P. longimembris, and Tucker (1965) gives values of 0.72 to 0.91 C/min for P. californicus, measured over small intervals of time. In fact, the values

reported by Tucker exceeded the theoretical values based on maximum heat production and minimum conductance. P. hispidus aroused spontaneously at an average rate of 0.27 C/min, but maximum rate was 0.50 C/min. When disturbed, the maximum rate of arousal was 0.8 C/min (Wang and Hudson, 1970). Hayden and Lindberg (1970) give an average value of 0.42 C/min for P. parvus which is within the 95% confidence limits for my data.

Oxygen consumption during the shivering phase of arousal is 7.28 ml/g/hr, and the corresponding value before shivering commences is 5.08 ml/g/hr.

The average total cost of arousal is 0.99 cal/g/C increase of T_B. Since the specific heat of mouse tissue is 0.83 cal/g/C (Hart, 1950), it appears that P. parvus is very efficient in utilizing its metabolic heat in the arousal process.

Examination of the data on R.Q. during torpor shows that an extremely low R.Q. is associated with torpor at low temperatures. It is not likely that these low values reflect accurately the substrate being metabolized. Although it would be possible, theoretically, to obtain a long-chain fat that could give values significantly lower than 0.70, there is no good evidence that this is the case. It is more likely that a reduced circulation to the skeletal muscles creates anaerobic conditions and enhances the glycolytic pathway, leading to the accumulation of lactate. This hypothesis is

supported by the fact that the R.Q. increases dramatically during the shivering phase of arousal (Fig. 7). Agid and Ambid (1969) report low R.Q. for the torpid dormouse, and Yousef et al. (1967) report values as low as 0.50 for torpid hamsters. In both cases the R.Q. increased during arousal, but it is not possible to ascribe these changes to the hypothesized anaerobiosis. Twente and Twente (1968) found no increase in tissue lactate in hibernating Citellus. It is not possible, at this time, to explain the extremely low R.Q. in torpid P. parvus, but a low R.Q. seems to be typical for the torpid state. Hibernators may have metabolic pathways for fixation of CO_2 into useful compounds.

Pulmo-cutaneous Water Loss

Schmidt-Nielsen and Schmidt-Nielsen (1951) computed the caloric intake, water intake, metabolic water production, and urinary water loss for kangaroo rats on a diet of dry pearl barley. The net water gain under these conditions was 0.102 mg H_2O/cal, indicating that a dry diet would be sufficient if no other water losses were incurred. However, it is obvious that some loss must occur through the pulmonary and cutaneous routes. Since a net gain is possible after subtracting water needed to excrete the ingested nitrogen and salts, the pulmonary and cutaneous routes of water loss assume a position of extreme importance to the desert rodent. The magnitude of these losses will determine the water

balance of the animal. It is necessary to examine the manner in which these losses are related to environmental parameters, especially ambient temperature and humidity. The data from this study relate pulmo-cutaneous water loss to ambient temperature only, and they are valid only at 0% relative humidity.

Pulmo-cutaneous water loss is expected to be controlled by several factors: ambient temperature, absolute humidity, metabolic rate, temperature of the expired air, and surface area of the skin. We can expect the respiratory, or pulmonary, water loss to be determined by the amount of moisture in the expired air, saturated at the temperature of the expired air, less the amount of moisture in the inspired air. The cutaneous loss should be a function of skin area and the humidity of the surrounding air. Since heteromyid rodents do not have sweat glands, there should be little or no increase in cutaneous water loss with increased metabolic rate. The ratio of cutaneous loss:pulmonary loss was found to be 28:72 at 20 - 25 C. As metabolic rate increases, with a concomitant increase in pulmonary loss, the effect of cutaneous loss becomes relatively less important to the total water economy of the animal.

The plot of raw data (mg H_2O/hr) for non-torpid animals in Fig. 8 gives an extremely wide spread of points. The regression line has a slight negative slope. Since metabolic rate increases much faster with

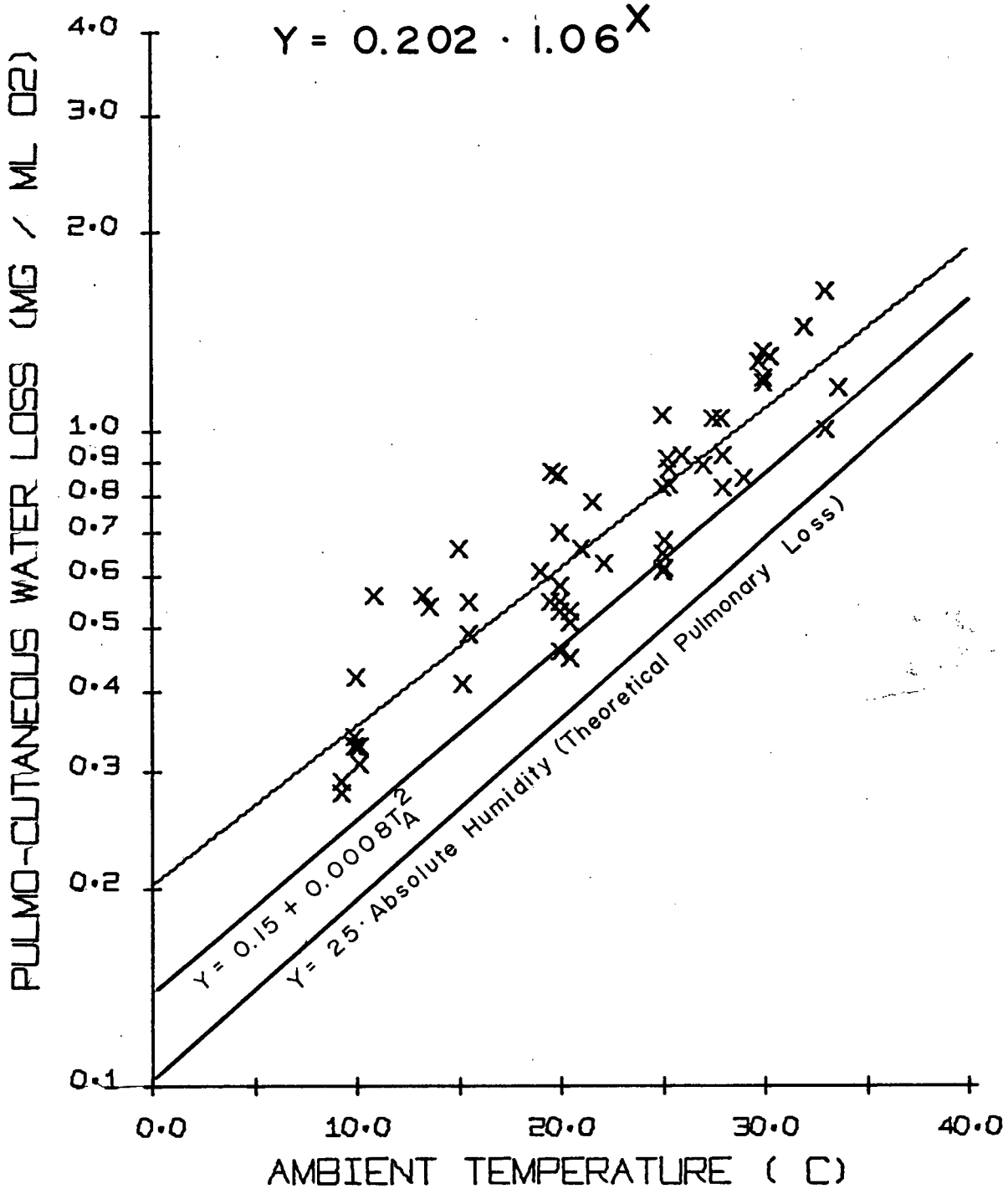
decreasing T_A, than does the observed water loss, this indicates that the animals are not saturating the expired air at body temperature, but at some lower temperature. Unless the animals have some means of super-cooling the nasal passages, this saturation temperature will be limited by T_A. This question has been investigated by Getz (1968), who found that the nasal temperature of Clethrionomys gapperi and Peromyscus leucopus was 0.-.9 C above T_A over the range of 5 - 30 C. More recently, Schmidt-Nielsen et al. (1970) have demonstrated that a counter-cooling mechanism does exist in the nasal mucosa of birds and mammals. The kangaroo rat exhaled air at a temperature lower than T_A, indicating that it does "super-cool" the expired air. This enables the animal to recover 54% to 83% of the water in the expired air.

A semi-logrithmic plot of the data from Fig. 10 produced a linear relationship as shown in Fig. 22. Since many factors can increase the pulmo-cutaneous water loss of an animal (e.g. panting), it is easier to overestimate than to under-estimate this loss. Moreover, the minimum values are more useful in evaluating the potential performance of a species than are the average or maximum values. The minimum values for pulmo-cutaneous water loss are adequately described by the equation $mg/ml = 0.15 + 0.0008\ T_A^2$. This parabolic function, fitted to the arithmetic plot of the data (Fig. 10),

FIG. 22

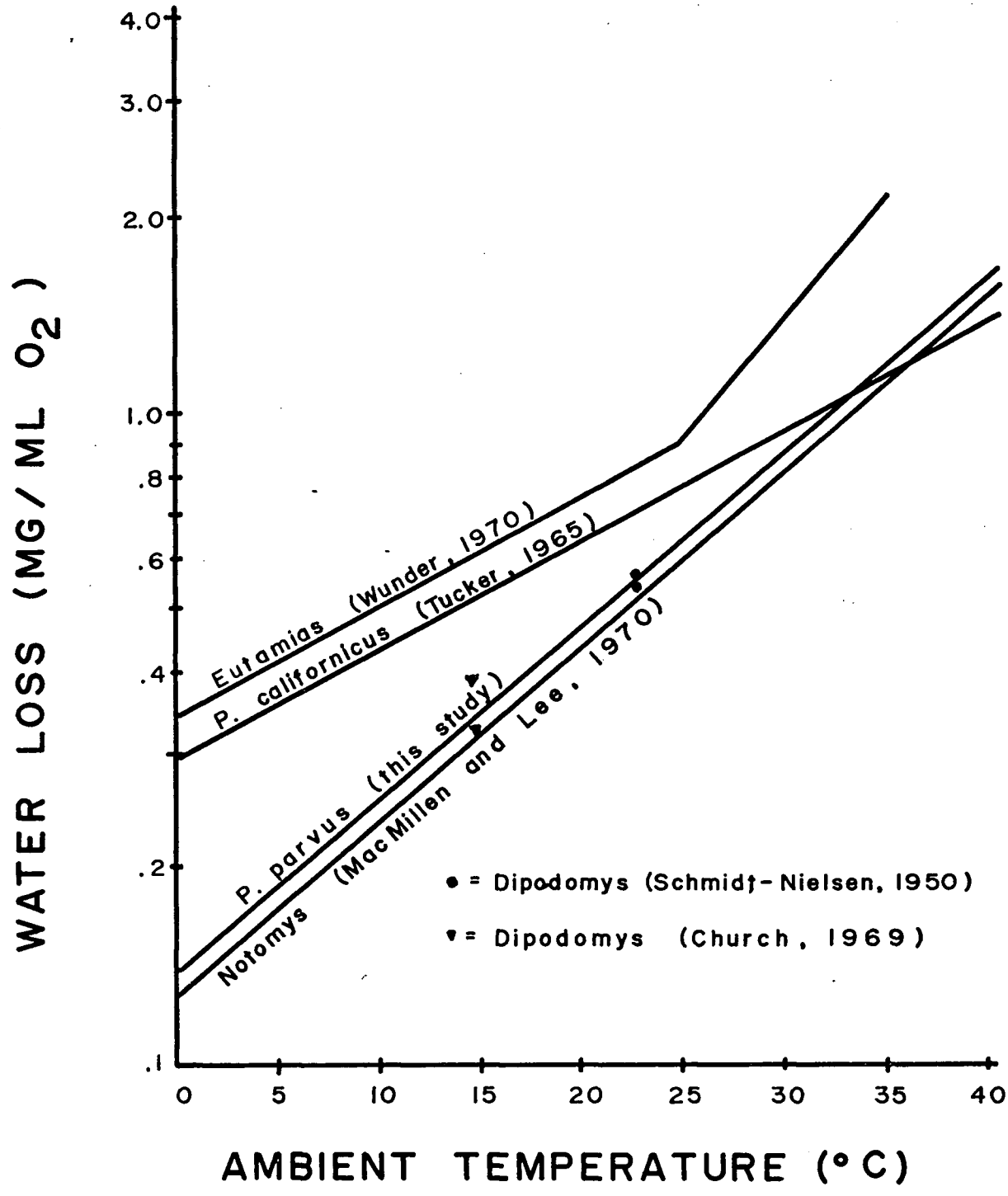
RELATIONSHIP OF RELATIVE PULMO-CUTANEOUS WATER LOSS OF NON-TORPID ANIMALS TO AMBIENT TEMPERATURE

LOG Y = -0.6942 + 0.0242X N = 56



provides a plot that is a straight line on a semi-log plot, over the pertinent range of temperatures of 10-30 C. The slope of this line on the semi-logarithmic scale is almost identical to the slope of the least squares regression. Fig. 23 compares the relationship of minimum pulmo-cutaneous water loss to ambient temperature for several other small mammals, as well as P. parvus. The curves for Notomys (a small, desert-adapted, Australian, Murid rodent) (MacMillen and Lee, 1970) are essentially identical to the curve for P. parvus in both slope and level. The curves for P. californicus and Peromyscus eremicus seem to differ from that of P. parvus in having less slope and a slightly higher level. Since both these species exhibit torpor only at temperatures above 15 C and inhabit more southerly deserts, the lower water loss for P. parvus at lower temperatures may indicate a superior adaptation for the colder areas that it inhabits. Many more data would be needed to support such a hypothesis. Eutamias (Wunder, 1970), in contrast to the other species, appears to have a change in slope at about 25 C. This coincides with a lower metabolic rate from about 25-35 C. Since the relative water loss (mg/ml O_2) increases when O_2 consumption decreases, it is logical to assume that the cutaneous loss component is higher in Eutamias than in the desert species. Values for Dipodomys venustus and D. merriami at 15 C (Church, 1969) and for D. spectabilis and D. merriami at 13 C (Schmidt-Nielsen and Schmidt-Nielsen, 1950)

FIG. 23 MINIMUM PULMO-CUTANEOUS WATER LOSS FOR SEVERAL SPECIES OF SMALL MAMMALS



are shown also in Fig. 23. These values coincide with the data from this study.

1. Cutaneous water loss

Fig. 14 shows that minimum cutaneous loss has a logarithmic relationship to ambient temperature; the equation for minimum values is $Y = 3.76 \cdot 0.0155^{X}$, where Y is mg H_2O/hr and X is T_A in C. The slope of this line is much less than the slope of the absolute humidity curve, indicating that the skin and fur are very effective in "insulating" the animal from the desiccating influence of low humidity. The fur probably exerts a major influence on cutaneous loss by increasing the diffusion path and reducing the gradient, but no data were collected on clipped animals to investigate this possibility.

2. Separation of cutaneous and pulmonary losses

The curve representing 25 x absolute humidity at T_A of 0-40 C did not provide as good a lower limit for the relative pulmocutaneous water loss data as did the curve $Y = 0.15 + 0.0008\ T_A^2$. Since the pulmonary efficiency of mammals is about 20% (Hughes, 1963) and the air contains approximately 20% O_2, the animal would respire 100 ml of air to extract 4 ml O_2. If the expired air is saturated at T_A, then 25 x absolute humidity should estimate the actual pulmonary loss. The discrepancy between the theoretical and empirical curves is expected, since both pulmonary and cutaneous losses increase logarithmically

with T_A, and the empirical curve is a summation of the pulmonary and cutaneous losses. If the minimum curves for cutaneous loss (Fig. 14) and pulmo-cutaneous loss (Fig. 22) are accurate, and if the pulmonary loss is described by the function, mg/ml = 25 · absolute humidity, the summation of minimum cutaneous loss and minimum pulmonary loss should approximate the curve fitted to minimum pulmo-cutaneous loss (i.e. $Y = .15 + .0008\ T_A^2$). Using the average metabolic rate curve and average body weight (17 g), I have computed the theoretical pulmonary and cutaneous losses over the range of T_A of 0-35 C. These values were summed and expressed as mg/ml O_2. Fig. 24 compares this summation with the line fitted to the original data. The computed values correspond very closely to the curve $Y = 0.15 + 0.0008\ T_A^2$, except at the higher values of T_A. The computed values would suggest that the slope of the fitted line is somewhat low.

Similar values were computed for a 17 g mouse in torpor, with the values expressed as mg/hr. Fig. 25 shows that the computed values are in agreement with the minimum values for pulmo-cutaneous loss of torpid animals from Fig. 11.

The general agreement between the minimum values from the data and the predicted values based on minimum cutaneous loss and the estimated mucosal temperature (mucosal temperature = T_A), supports the reliability of the original data and the minimum curves fitted to them.

FIG. 24 COMPARISON OF OBSERVED PULMO-CUTANEOUS LOSS WITH PREDICTED LOSS, BASED ON THEORETICAL PULMONARY LOSS + CUTANEOUS LOSS FROM FIG. 14 (NON-TORPID)

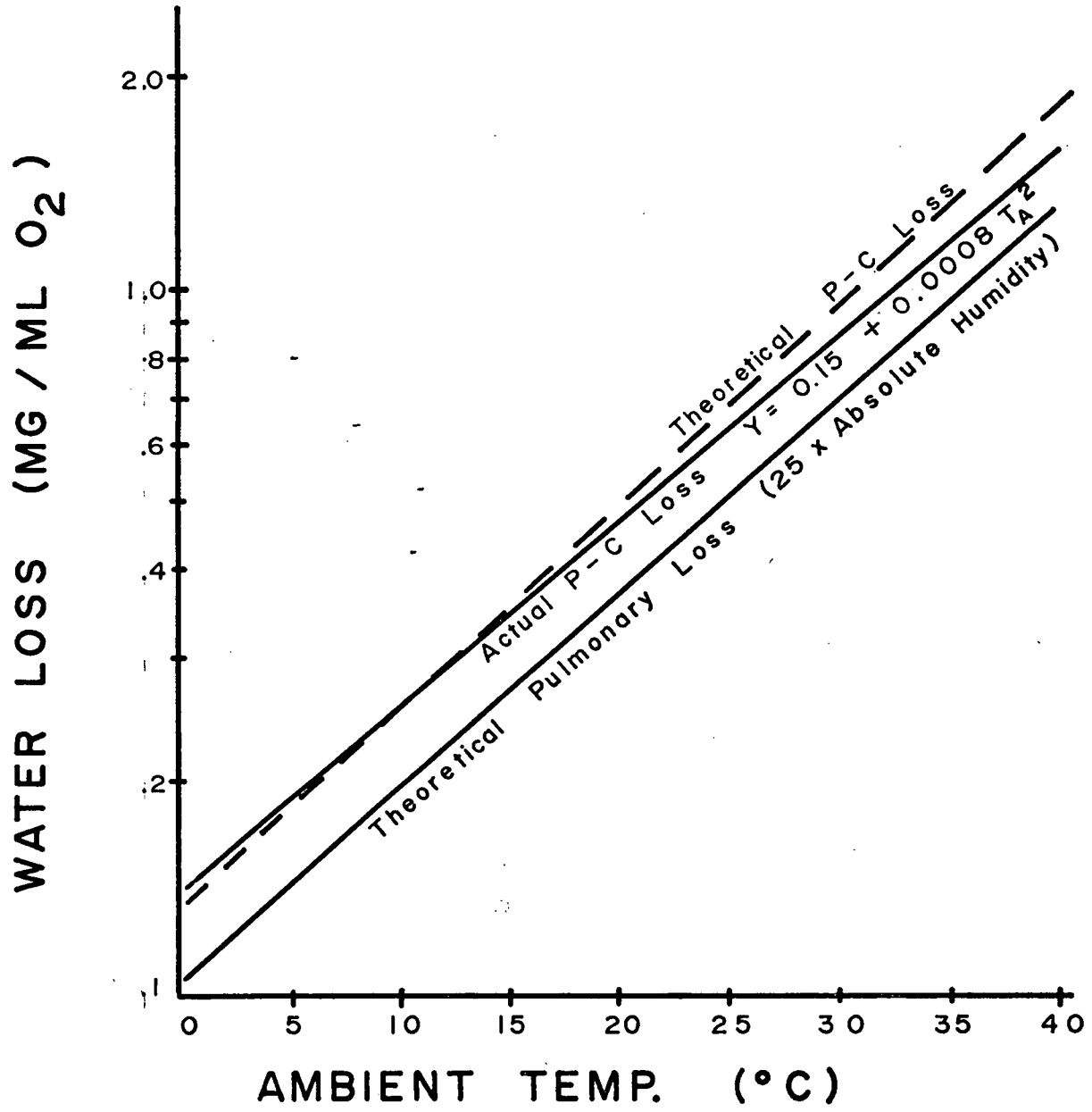
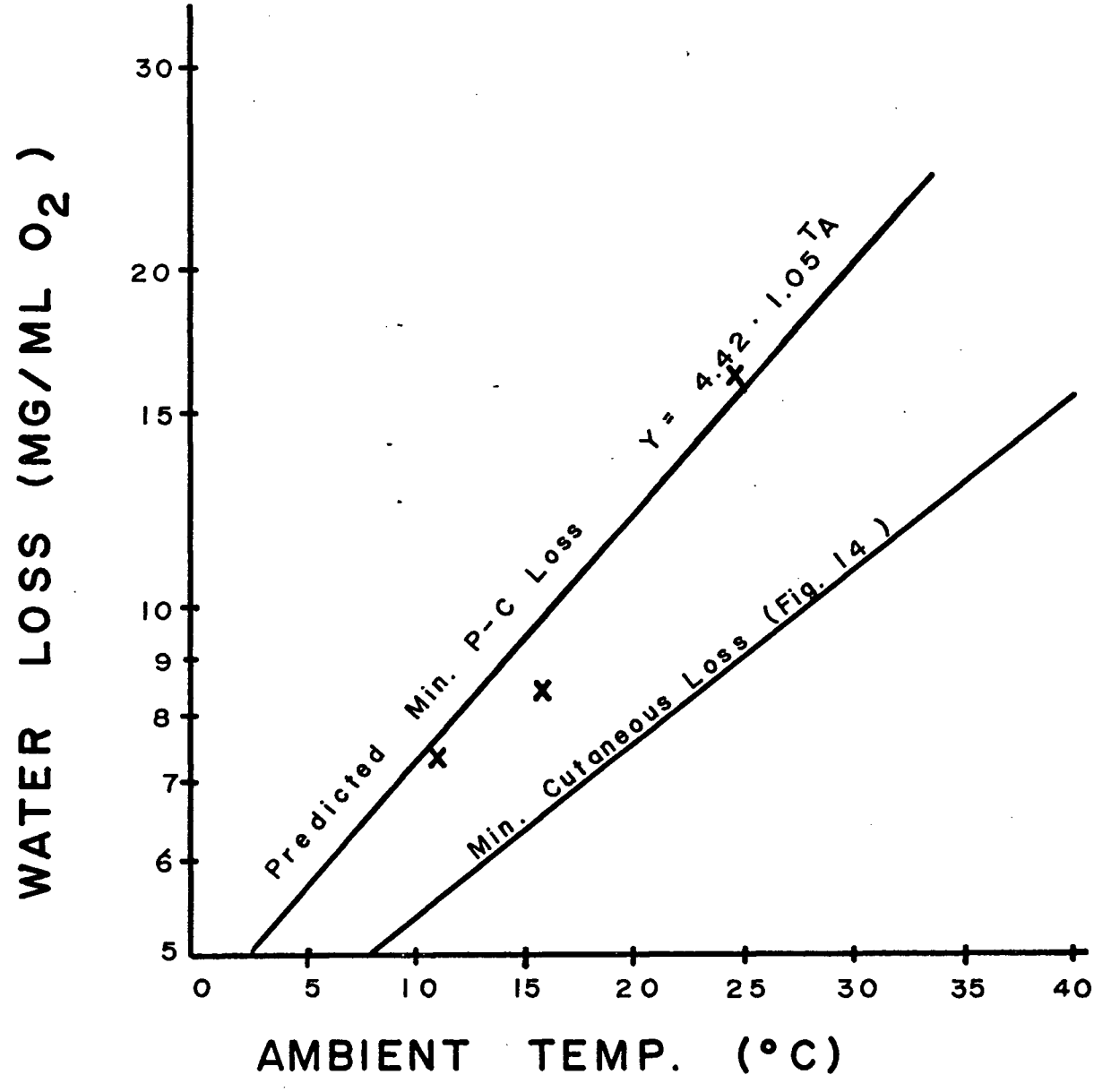


FIG. 25 COMPARISON OF MINIMUM PULMO-CUTANEOUS OF TORPID ANIMALS (x) WITH MIN. PREDICTED VALUES, BASED ON CUTANEOUS LOSS (FIG. 14) AND ON THEORETICAL PULMONARY LOSS



Hopefully, more comprehensive studies of water loss in small desert rodents will be forthcoming. It will be most interesting to see comparisons between these data and data collected with newer, more sophisticated techniques, such as the isotope technique used by Mullen (1970).

Energy and Water Budgets

It is easier to comprehend visual relationships than purely conceptual relationships. Thus, to transform these data to a visual form, I have constructed models which estimate the energy requirements and water losses of an animal at any given T_A and at any given amount of torpor. This model may be useful as a predictive model, but it cannot be so considered until it is tested. These limitations of the model are rather severe, since it does not include activity and does assume 0% relative humidity. Neither of these restrictions is true in the field, so any predictions to the field situation would require extremely careful study. The main advantage of the model is the provision of a three-dimensional display of the data, although I hope that others will construct refined versions for true predictive use under field situations.

1. Energy budget model

In view of the large number of variables, it was necessary to simplify the model as much as possible

in order to produce a manageable equation. This model, of course, is merely one of many possible, equally valid estimates of the energy expenditure for this species. To simplify the model, the following assumptions were made:

1. No component for activity is included.
2. Entry and arousal occur, even when the time in torpor = 0.
3. Entry time is constant at 1.5 hr.
4. Energy consumption during entry averages 35% of normal consumption at the entry T_A.
5. Arousal time is constant at 1.1 hr.
6. Metabolic cost of arousal is 1.00 cal/g/C.
7. Maximum time in torpor is limited to 140 hr/week.
8. Metabolic rate in torpor = $1.81 + 0.068\ T_A$, with M.R. in cal/g/hr.
9. Normothermic M.R. = $40.45 - 1.127\ T_A$, with M.R. in cal/g/hr.

The following variables were selected:

X = hours in torpor/bout (length of torpor period)
Vary from 0 to 140.

Y = Ambient temperature
Vary from 0 to 30 C.

Z = Total calories/week

N = Number of torpor periods/week.

W = Body weight.

The equation, after simplification, becomes:

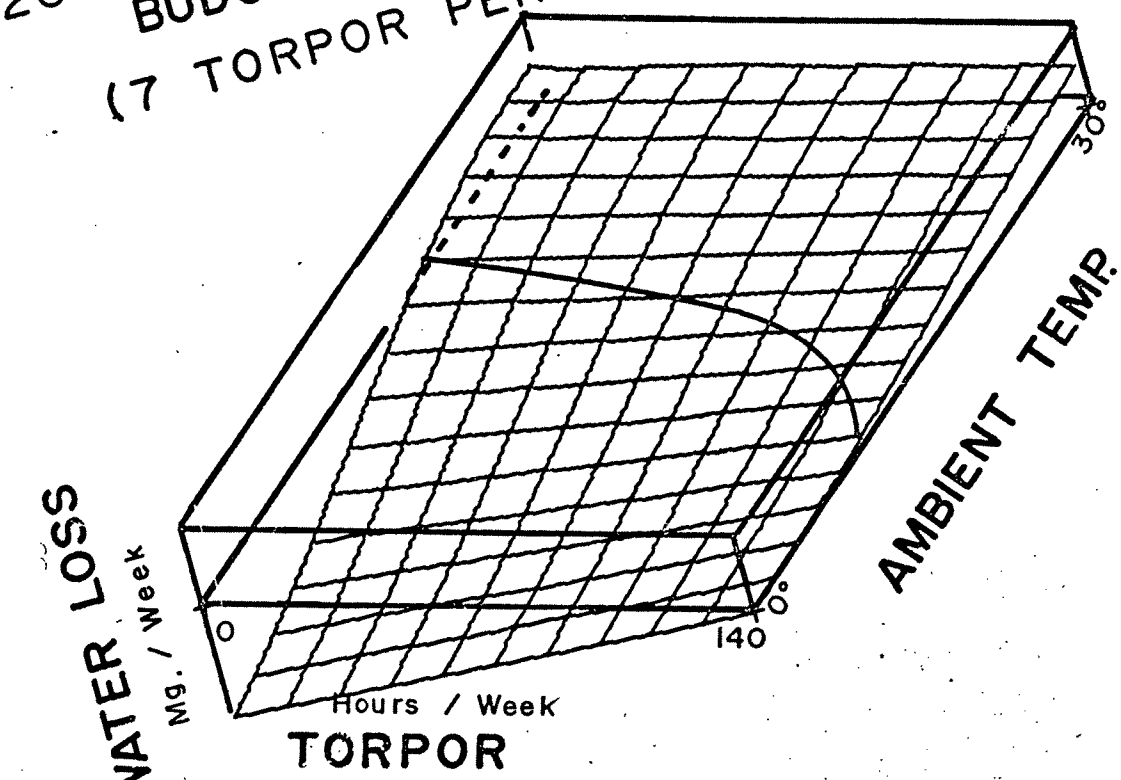
$$\text{calories/week} = N\,W\,(21.5 - 0.6\,Y) + N\,W\,(35 - Y) + N\,W\,X\,(1.81 + 0.068\,Y) + [W\,(40.45 - 1.127\,Y)]\,[168 - N\,X - 2.5\,N]$$

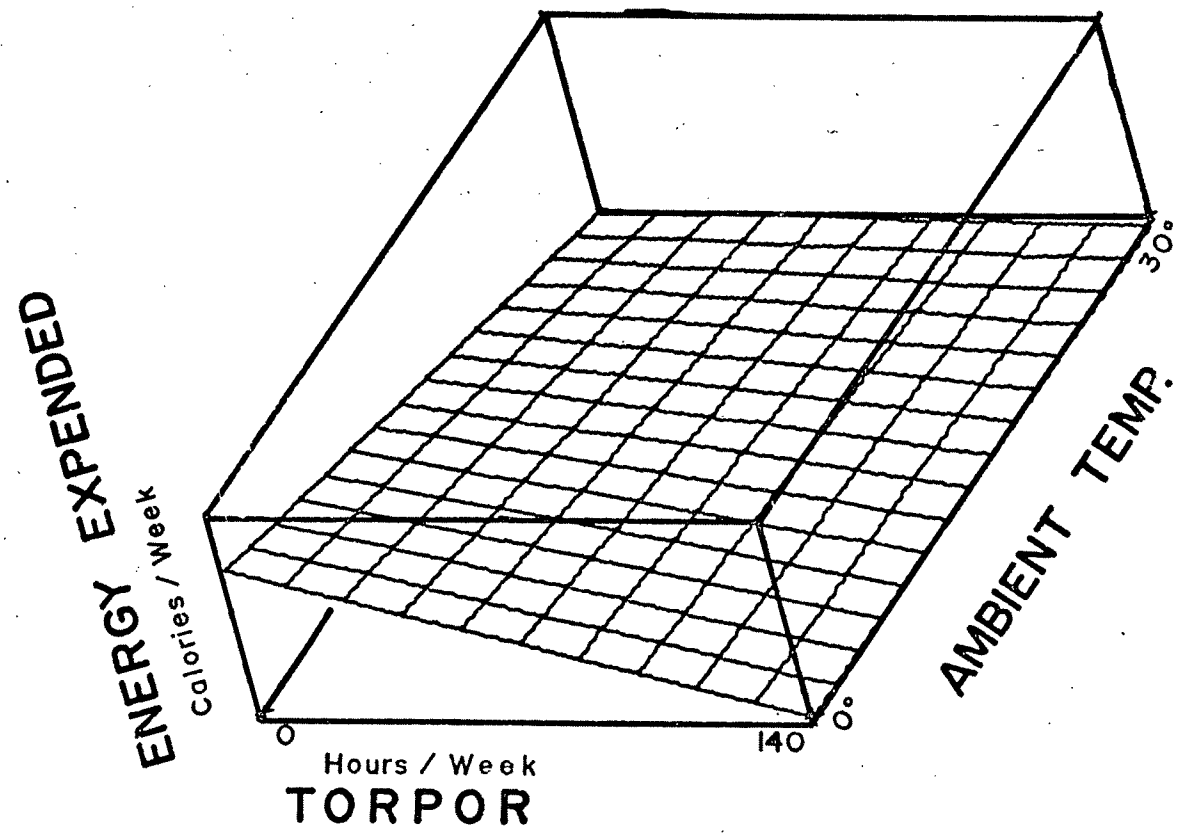
Three-dimensional plots of this model for a 17 g animal are shown in Fig. 26 for 7 bouts of torpor/week, and Fig. 27 for 1 bout of torpor/week. The model is a tilted plane, with highest point at 0 C and 0 hr of torpor, and lowest point in the opposite corner at 30 C and 140 hr of torpor/week. The maximum hours of torpor per week was set at 140 because this is the maximum continuous torpor observed for this species by Iverson (1967) or by me. In reality, this figure could be higher since an animal might arouse after 140 hr and re-enter torpor immediately. Thus, the requirement that an animal spend 28 hr/week in the non-torpid state tends to increase the predicted energy expenditure at maximum torpor above the values that could occur in a field situation.

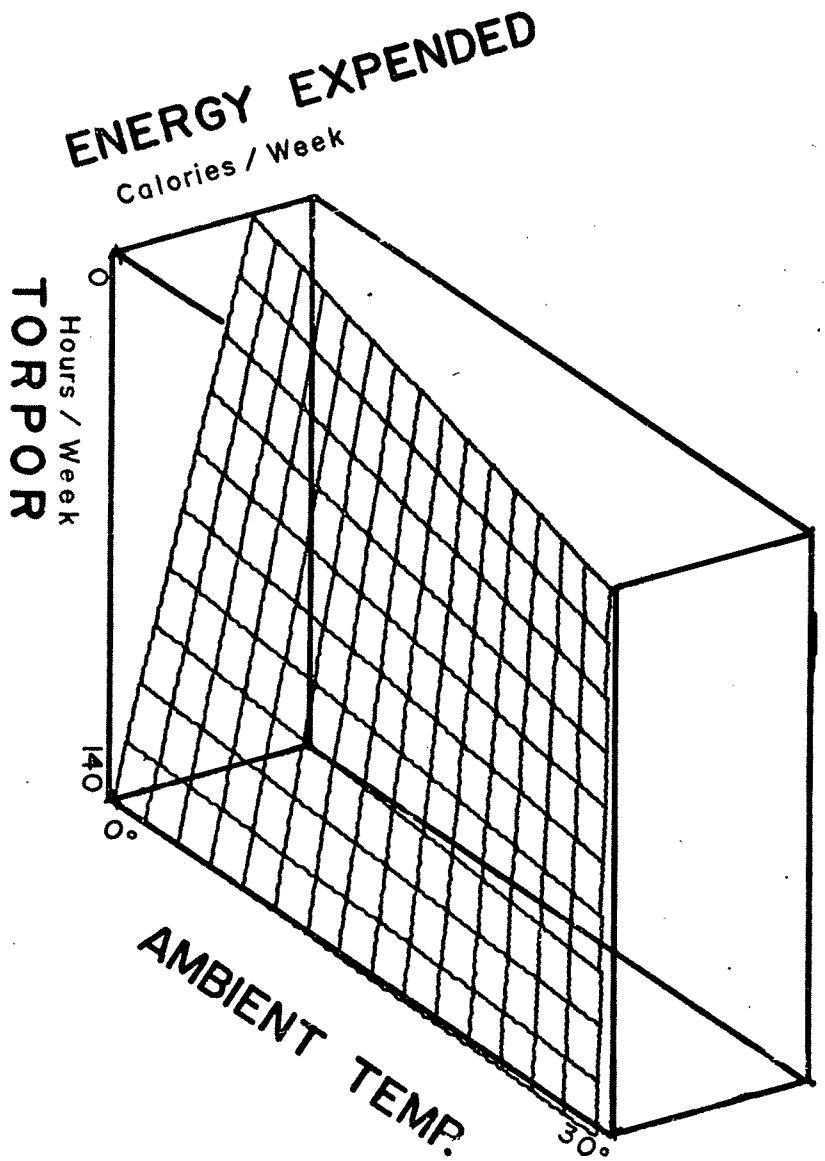
2. Water-loss model

Since the main loss of water in P. parvus is pulmo-cutaneous loss, and since the main source of water is metabolic water, it is obvious that the net loss is some function of daily metabolism. Thus, the energy model, detailed previously, becomes an important structural unit in this model. Since composition of diet influences the amount of metabolic water produced, it is necessary to select a constant diet in the construction of the model.

FIG. 26 ESTIMATED ENERGY AND WATER BUDGETS (17 G. ANIMAL) (7 TORPOR PERIODS / WEEK)







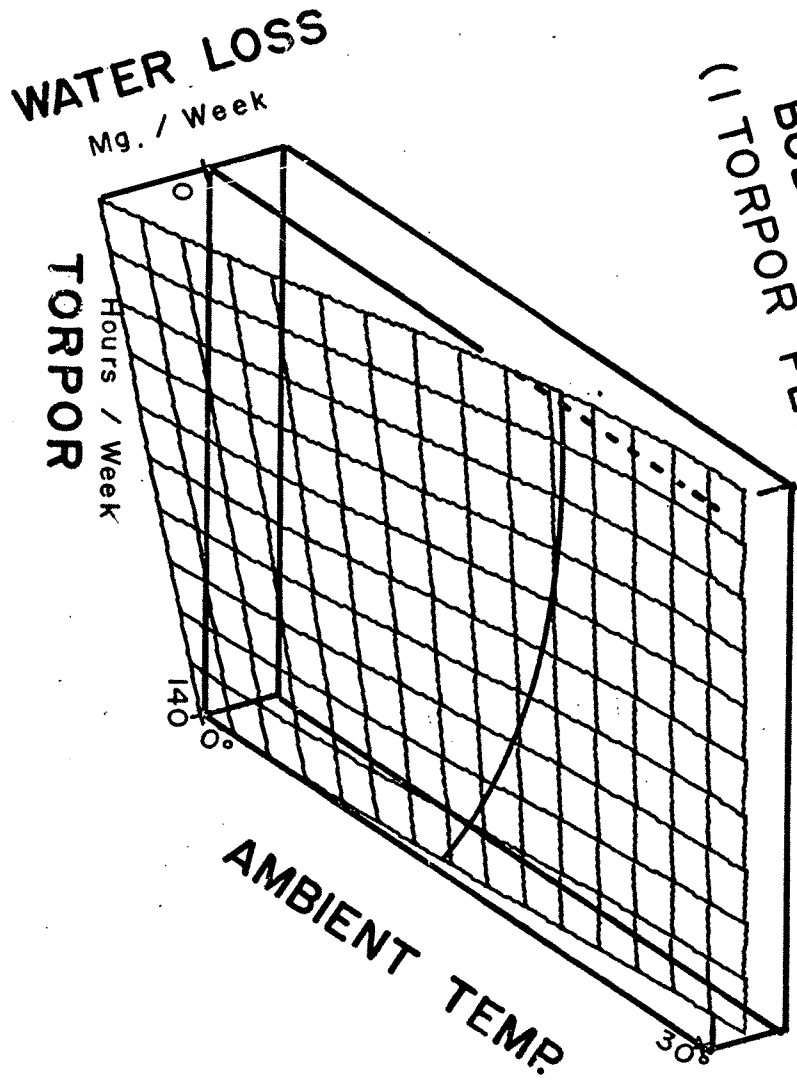


FIG. 27 ESTIMATED ENERGY AND WATER BUDGETS (17 G. ANIMAL) (1 TORPOR PERIOD / WEEK)

In this model, the pearl barley diet detailed by Schmidt-Nielsen and Schmidt-Nielsen (1951) will be used. Other data published by these authors, notably maximum urine concentration for Perognathus, will be used in constructing the model. This model, of course, is valid only at 0% relative humidity.

The following assumptions will be made:

1. Pulmo-cutaneous water loss of non-torpid animals is determined by M.R. · mg H_2O lost/ml O_2 consumed.
2. Mg/ml = $0.15 + 0.0008\ T_A^2$
3. Pulmo-cutaneous loss in torpid animals is estimated by: mg/hr = $4.42 \cdot 1.05^{T_A}$.
4. Urinary water loss = 3.4 mg/100 cal.
5. Fecal water loss = 0.7 mg/100 cal.
6. 20.4 ml O_2 is required to metabolize 100 cal.
7. Metabolic water = 13.4 mg/100 cal.
8. Preformed water in food = 0.9 mg/100 cal.
9. The relative pulmo-cutaneous water loss (mg/ml O_2) is the same during arousal and entry as for the non-torpid condition.

Using these assumptions, one can construct the following components:

Evaporative water loss in torpor = $N \times (4.42 \cdot 1.05^{T_A})$.

Evaporative water loss, non-torpid =

$$\frac{\text{cal/week} - [N \times W\ (1.81 + 0.068\ T_A)]}{4.9} \cdot (0.15 + 0.008 T_A^2)$$

H_2O Loss	H_2O Gain
Urine = 3.4 mg/100 cal	Metabolic = 13.4 mg/100 cal
Feces = 0.7 mg/100 cal	Preformed = 0.9 mg/100 cal
TOTAL = 4.1 mg/100 cal	TOTAL = 14.3 mg/100 cal
	- 4.1
	NET GAIN = 10.2 mg/100 cal

Combining these components with the energy model produces a model for net water loss per week, where:

X = hours in torpor/bout — Vary from 0 to 140

Y = ambient temperature — Vary from 0 to 30 C

Z = net water loss/week (mg/week)

N = number of bouts of torpor/week

W = body weight (g)

The final equation becomes:

$$\text{mg } H_2O/\text{week} = N X (4.42 \cdot 1.05^{T_A}) + [0.0306 + 0.000163 Y^2][(168 - N X)(W)(40.45-1.127Y)] - 0.102 [N W (21.5 - 0.6 Y) + N W (35 - Y) + N W X (1.81 + 0.068 Y) + (W) (168 - N X - 2.5 N)(40.45 - 1.127 Y)]$$

Three-dimensional plots of this model for a 17 g animal are shown in Fig. 26 for 7 bouts of torpor per week and Fig. 27 for 1 bout of torpor/week. The model is a curved, tilted surface, with the lowest point at 0 C and 0 hr of torpor/week. At 0 hr of torpor, the animal passes from positive to negative water balance at about 20 C. This transition point is reached at a progressively lower T_A as hours of torpor increase, and the animal goes into negative water balance at 9 C and

and 140 hr/week (20 hr/day) in Fig. 26 and at 13 C and 140 hr/week in the continuous-torpor situation of Fig. 27. Thus, the data indicate that torpor is not a water-conserving mechanism. Torpor appears to provide a means of exchanging water for energy. The range of temperatures over which torpor is feasible without encountering negative water balance is increased considerably (from 9 C to 13 C) by reducing the number of bouts per week and simultaneously increasing the length of the torpor period. In other words, one long period of torpor is more economical of water than is the same amount of torpor divided into daily periods.

The relationship of water loss to energy conservation can be examined in a slightly different way. Fig. 28 shows the relationships of net water production and pulmocutaneous loss to ambient temperature for a 17 g, non-torpid animal. As mentioned previously, the transition from positive to negative water balance occurs at about 21 C. These same relationships are shown in Fig. 29 for a torpid animal of the same body weight. The water loss is always greater than water production under these conditions, and torpor is not conserving water. The differences between production and loss for the torpid and non-torpid conditions are shown in Fig. 30. This indicates that torpor is always more expensive, in terms of water, than the non-torpid state, but the difference becomes minimal at higher ambient temperatures. Thus,

FIG. 28 ESTIMATED WATER PRODUCTION AND PULMO-CUTANEOUS LOSS OF A 17-GM. MOUSE (0% r.h.; No Torpor)

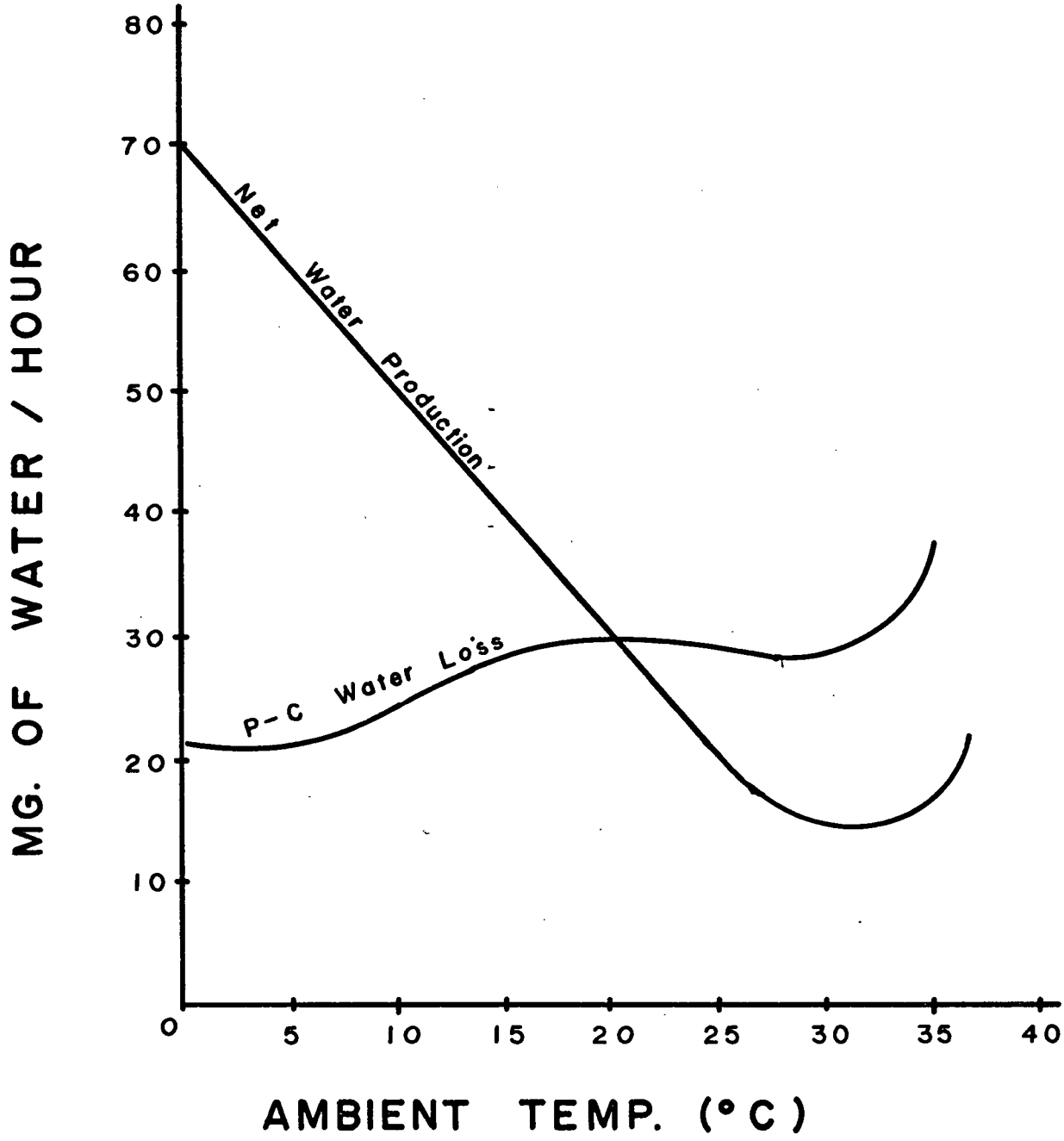


FIG. 29 ESTIMATED WATER PRODUCTION AND LOSS FOR A TORPID, 17-GM. MOUSE (0% r.h.)

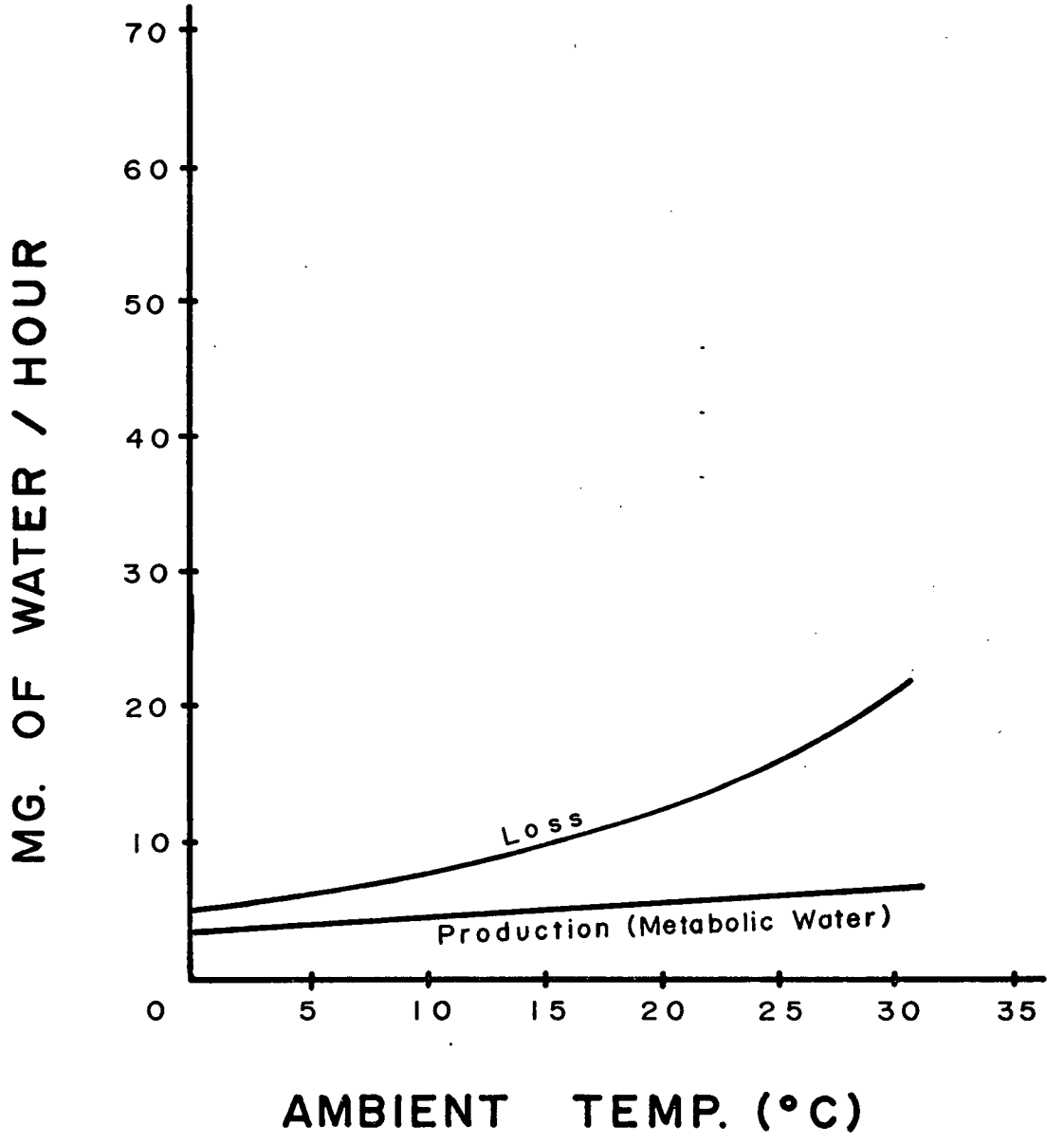
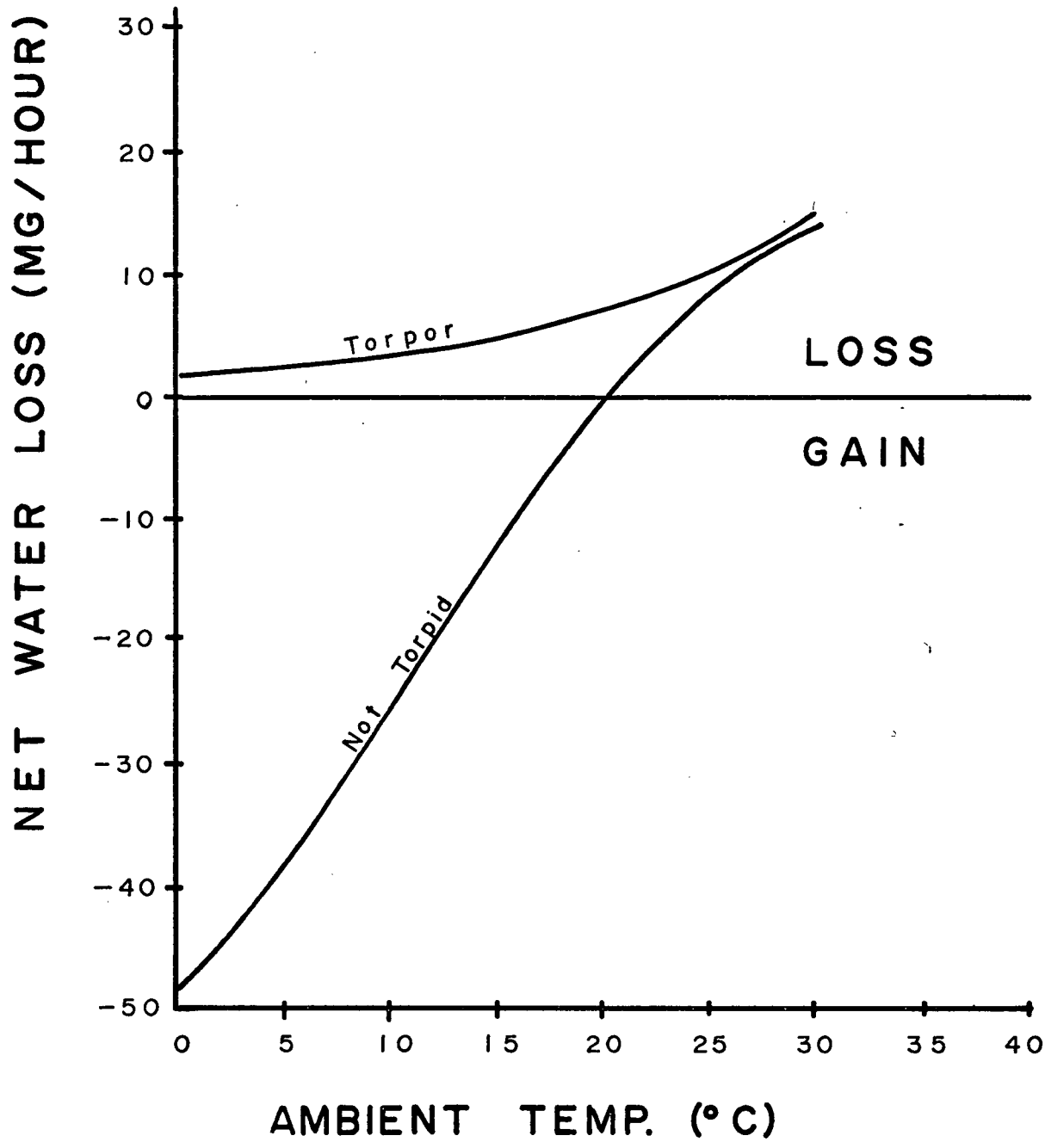


FIG. 30 NET WATER LOSS OF A 17-GM MOUSE IN THE TORPID AND IN THE ACTIVE STATE



we have a situation in which torpor conserves energy but expends water. Fig. 31 shows these relationships of energy conservation and water expenditure to ambient temperature. Having obtained these curves, we can express conveniently the cost of torpor by dividing the water expenditure by the energy conserved. The resulting curve, Fig. 32, expresses the cost of torpor as mg H_2O/kcal over ambient temperature. This curve indicates that the cost of torpor is minimal at 25 C with a range of low values extending from 20 - 30 C. Although torpor seems to be expensive at all ambient temperatures, "aestivation" would almost certainly occur within this low-cost range. This indicates that torpor, in P. parvus, is probably an energy-conserving mechanism with the cost, in terms of water, at a minimum during the hotter, drier season.

We can examine the effect of body size on water conservation during torpor by comparing the plots for the 17 g animal (Figs. 26 and 27) with similar plots for a 10 g animal (Figs. 33 and 34) and for a 25 g animal (Figs. 35 and 36). Examination of the zero-isolines shows that smaller animals are at a disadvantage. The 25 g animal appears to be capable of remaining in positive water balance during long-term torpor at temperatures up to 16 C, while the 10 g animal reaches its transition point at 7 C under the same conditions. This advantage of larger over smaller animals can be attributed to the

FIG. 31 ENERGY CONSERVED AND WATER EXPENDED BY TORPOR (17-GM MOUSE ; 0% r.h.)

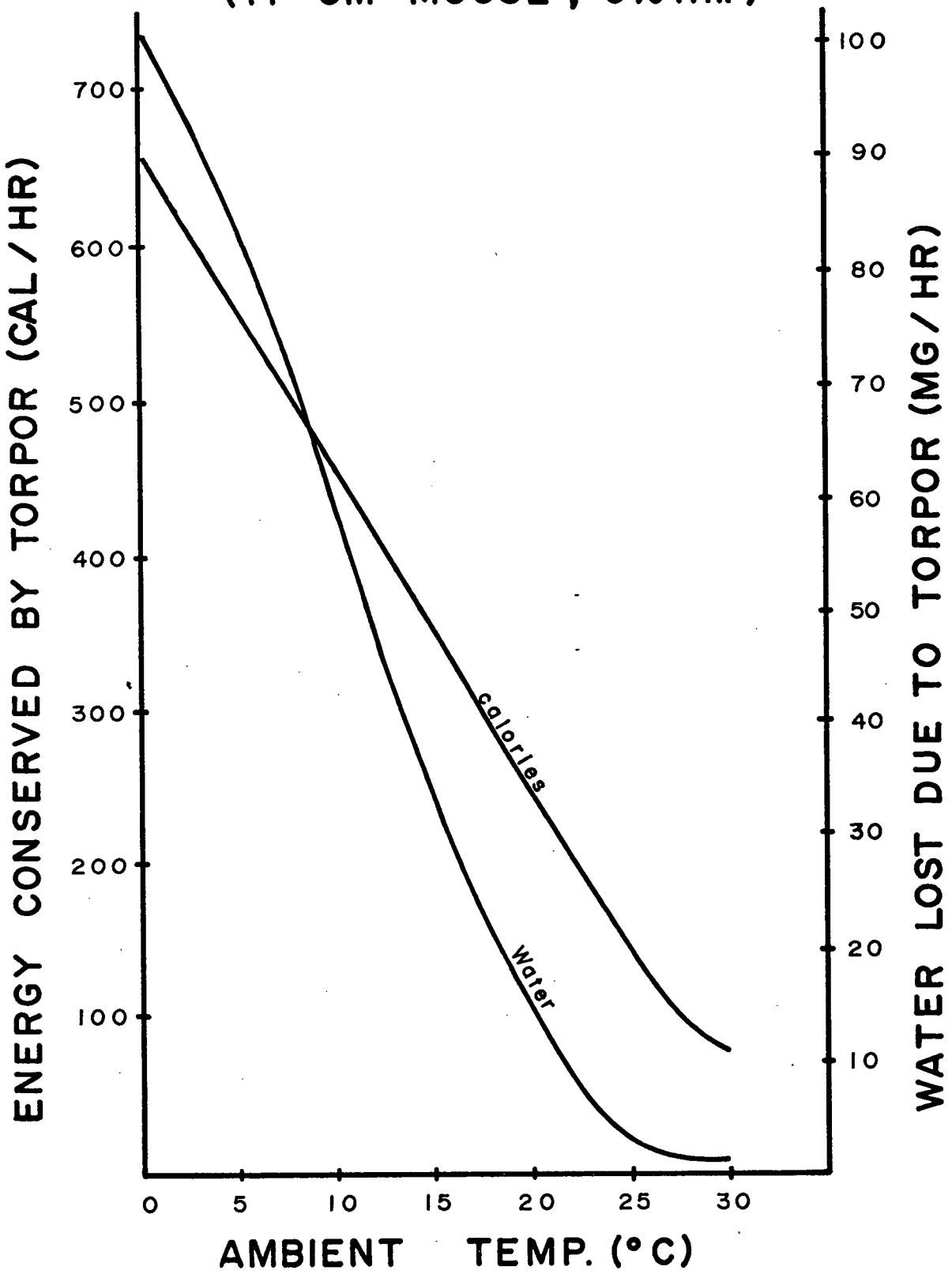


FIG. 32 COST OF CONSERVING ENERGY BY TORPOR (17-GM MOUSE; 0% r.h.)

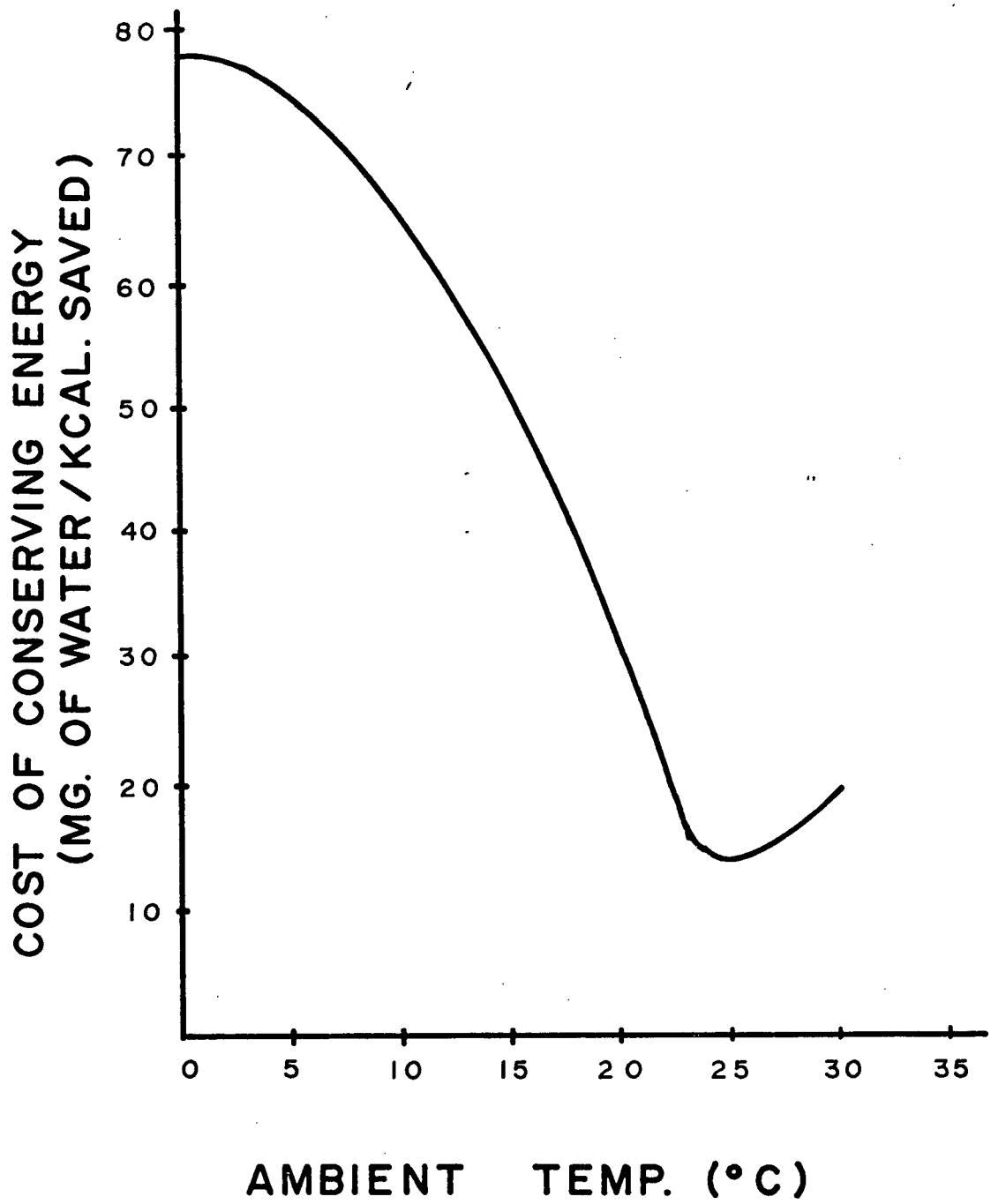


FIG. 33 ESTIMATED ENERGY AND WATER BUDGETS (10 G. ANIMAL) (7 TORPOR PERIODS / WEEK)

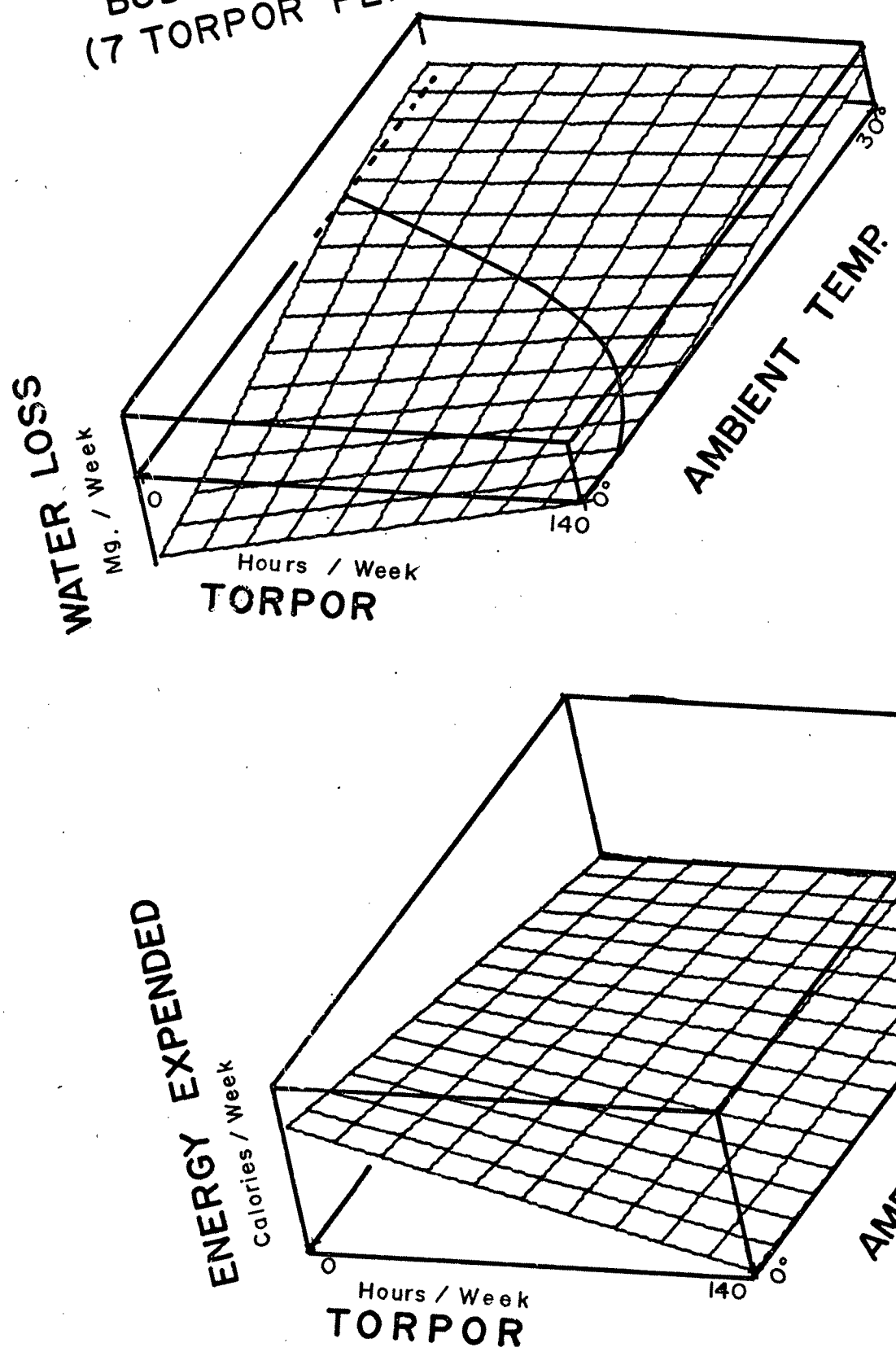


FIG. 34 ESTIMATED ENERGY AND WATER BUDGETS (10 G. ANIMAL) (1 TORPOR PERIOD / WEEK)

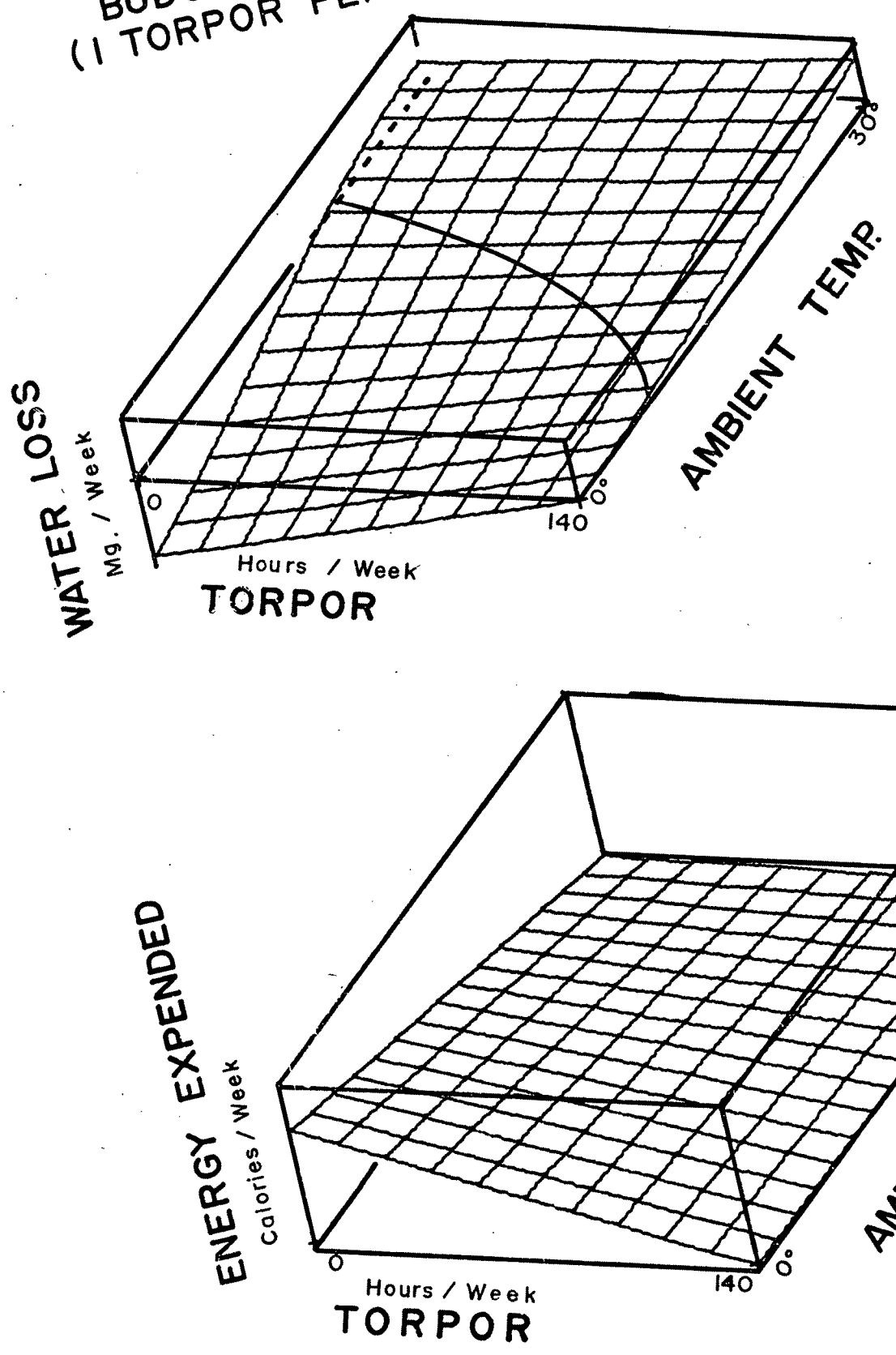


FIG. 35 ESTIMATED ENERGY AND WATER BUDGETS (25 G. ANIMAL) (7 TORPOR PERIODS/WEEK)

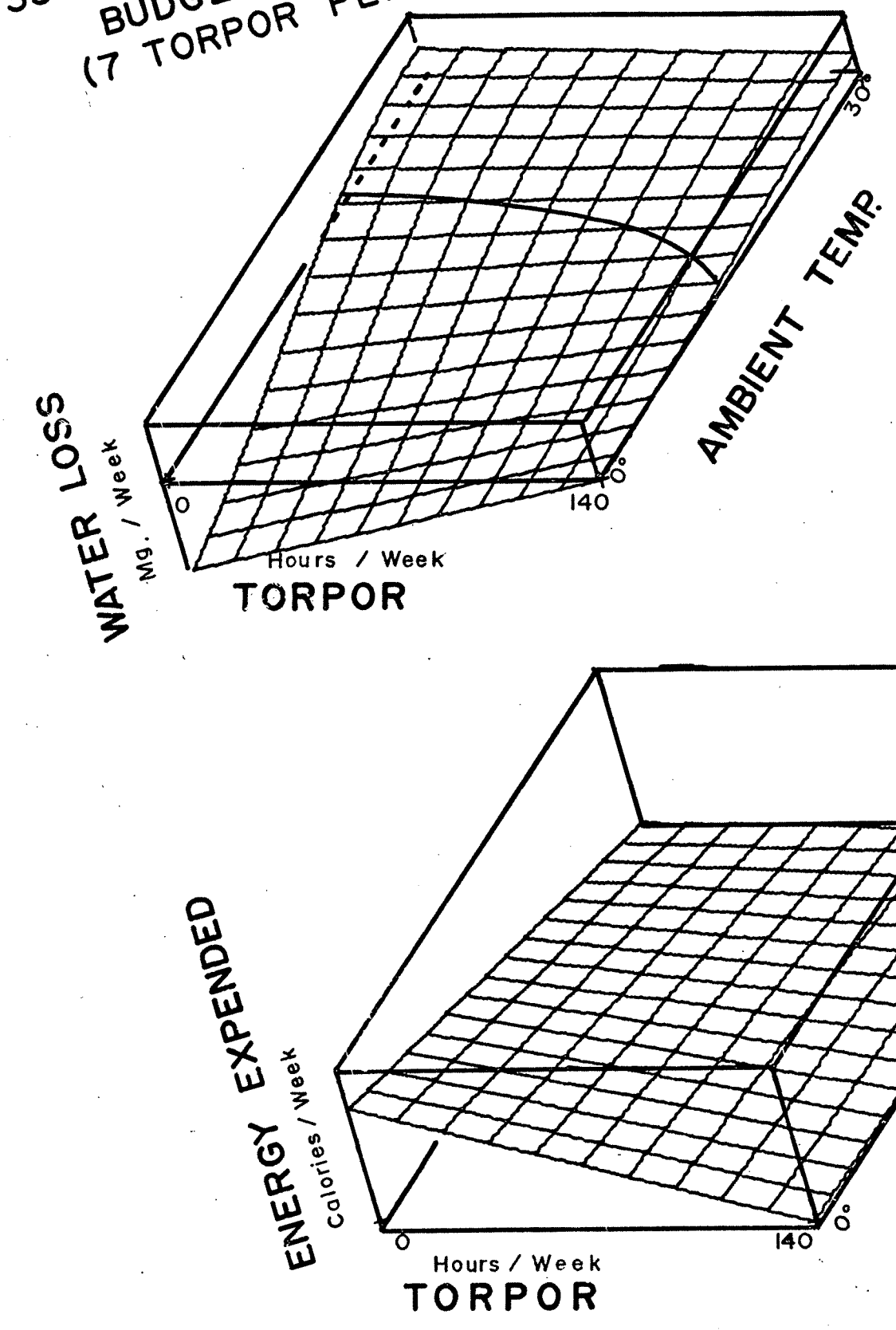
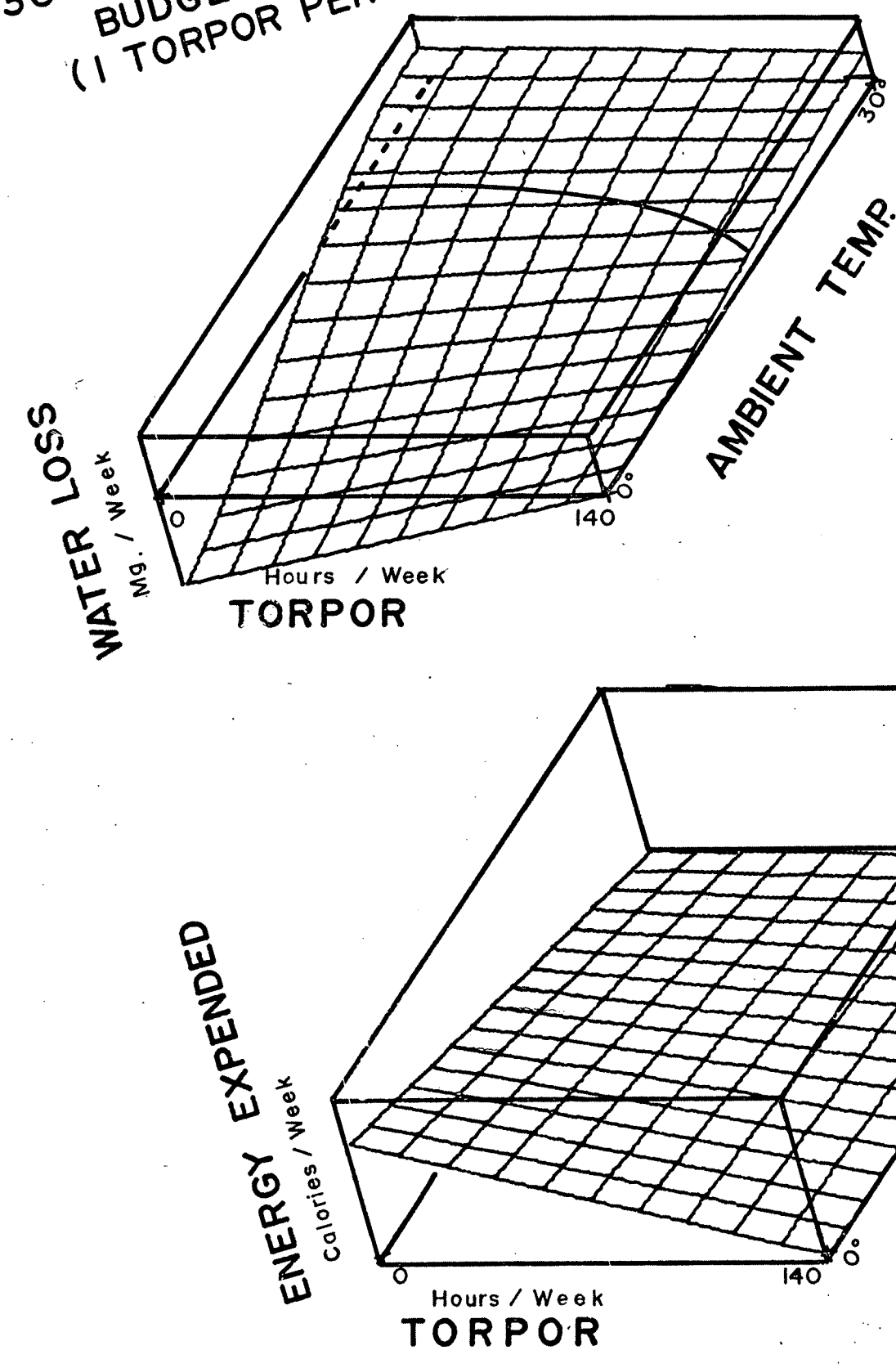


FIG. 36 ESTIMATED ENERGY AND WATER BUDGETS (25 G. ANIMAL) (1 TORPOR PERIOD / WEEK)



reduced surface:volume ratio of larger animals. The net metabolic water production is a function of mass, but cutaneous water loss is a function of surface area. As Fig. 15 shows, there is a very slight increase in surface area with increased body weight. A 10 g animal has 70% of the surface area but only 40% of the mass of a 25 g animal. It must be emphasized that the model is probably less accurate for body weights above or below the mean body weight (17 g). This will tend to under-estimate cutaneous loss for large animals and over-estimate for small animals, but the basic relationships will not be affected. Although these data fail to indicate the often-assumed benefit of torpor to the water budget, they suggest that larger animals, such as the ground squirrels, could benefit from torpor. This would be the case only if their cutaneous loss is low and their surface:volume ratio is also low.

Examination of the curves in Fig. 29 reveals that the transition from positive to negative water balance would occur at 23 C if there were no cutaneous loss. The cutaneous loss has the effect of shifting the transition point to a lower T_A. The evolution of low cutaneous water loss has enabled these desert animals to employ the energy-conserving device of torpor at higher ambient temperatures, without incurring a severe water loss. It is quite possible that energy is a more severe limiting factor than water for fossorial desert rodents.

All the data in this study, and therefore all the conclusions, were based on 0% relative humidity and no activity. Since these conditions rarely, if ever, occur in a natural situation, it is essential to estimate the manner in which field conditions will affect the conclusions. Burrow temperatures will vary from 0 C in winter to 25 C in summer (Brown and Bartholomew, 1969). The humidity in the burrow is expected to be 100% relative humidity (Schmidt-Nielsen and Schmidt-Nielsen, 1950). At 100% relative humidity the animal will lose little or no moisture through the pulmonary route (Schmidt-Nielsen et al., 1970), and the cutaneous loss probably will decrease to insignificant levels. Humidities greater than 0% would reduce cutaneous loss due to a reduction in the moisture gradient. The pulmonary loss would be reduced considerably due to the inspiration of water. However, the temperature of the nasal mucosa will increase since less evaporative cooling can occur. This will reduce the efficiency with which water is removed from the expired air. The total amount of water lost through the pulmonary route will be much reduced, but may be higher than expected if the change in mucosal temperature is not considered. Total water loss at elevated humidities will probably decrease as some function of the increase in humidity, becoming minimal at 100% relative humidity.

Activity can be estimated from data on metabolic rate for P. formosus under field conditions (Mullen, 1970). An isotopic method was used to estimate the metabolic rate of P. formosus. Since this species is similar to P. parvus

in habits and size, it is reasonable to compare the data from this study with those for P. formosus. The field data indicate considerably higher values for metabolic rate than do lab data for resting metabolic rate. By subtracting the resting metabolic rate (this study) from the field metabolic rate (Mullen, 1970), we can obtain an estimate of activity. If the assumption is made that all activity energy is expended within a 3-hr period at 0% relative humidity, and that all other energy is expended in the burrow at 100% relative humidity, it is possible to estimate the effects on water loss. Fig. 37 shows the estimated net water production for a 17 g animal on a diet of pearl barley and the estimated pulmo-cutaneous loss, based on the assumptions mentioned. The difference between net production and pulmo-cutaneous loss, representing the net gain or net loss, is plotted in Fig. 38. Assuming that all torpor occurs at 100% relative humidity, the net water production becomes equivalent to a net gain. This relationship is also shown in Fig. 38. A comparison of the estimated net water gain in torpor with the estimated net gain of an active animal under the assumed field conditions, indicates that torpor continues to be expensive of water, relative to the active state. These estimates show that the basic relationships between torpid and active states, under field conditions, do not differ from the relationships determined under laboratory conditions, and they reinforce the conclusion that it is not likely that torpor has evolved as a water-conserving mechanism. However,

FIG. 37 ESTIMATED WATER PRODUCTION PULMO-CUTANEOUS LOSS FOR A 17-GM. MOUSE UNDER FIELD CONDITIONS

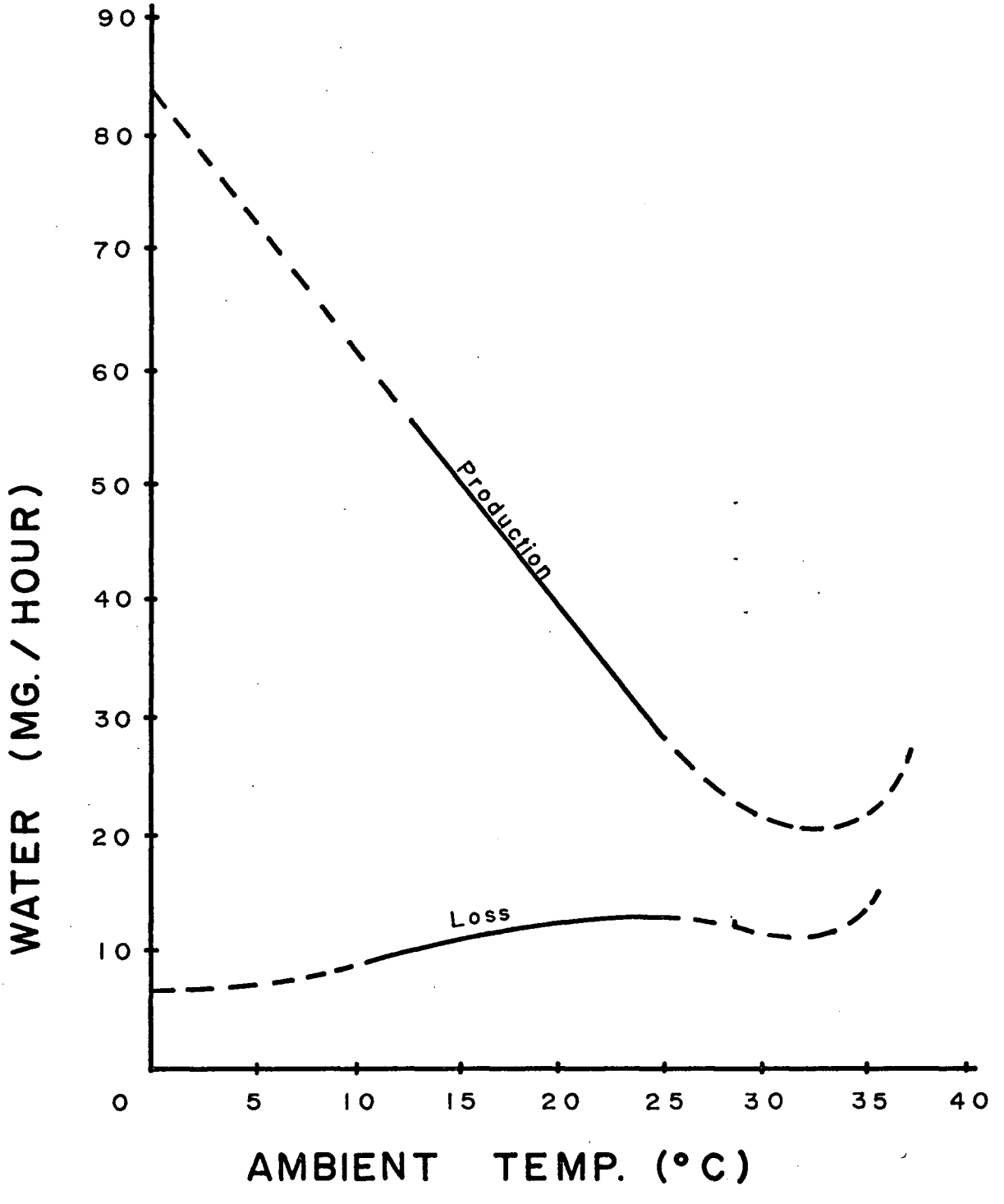
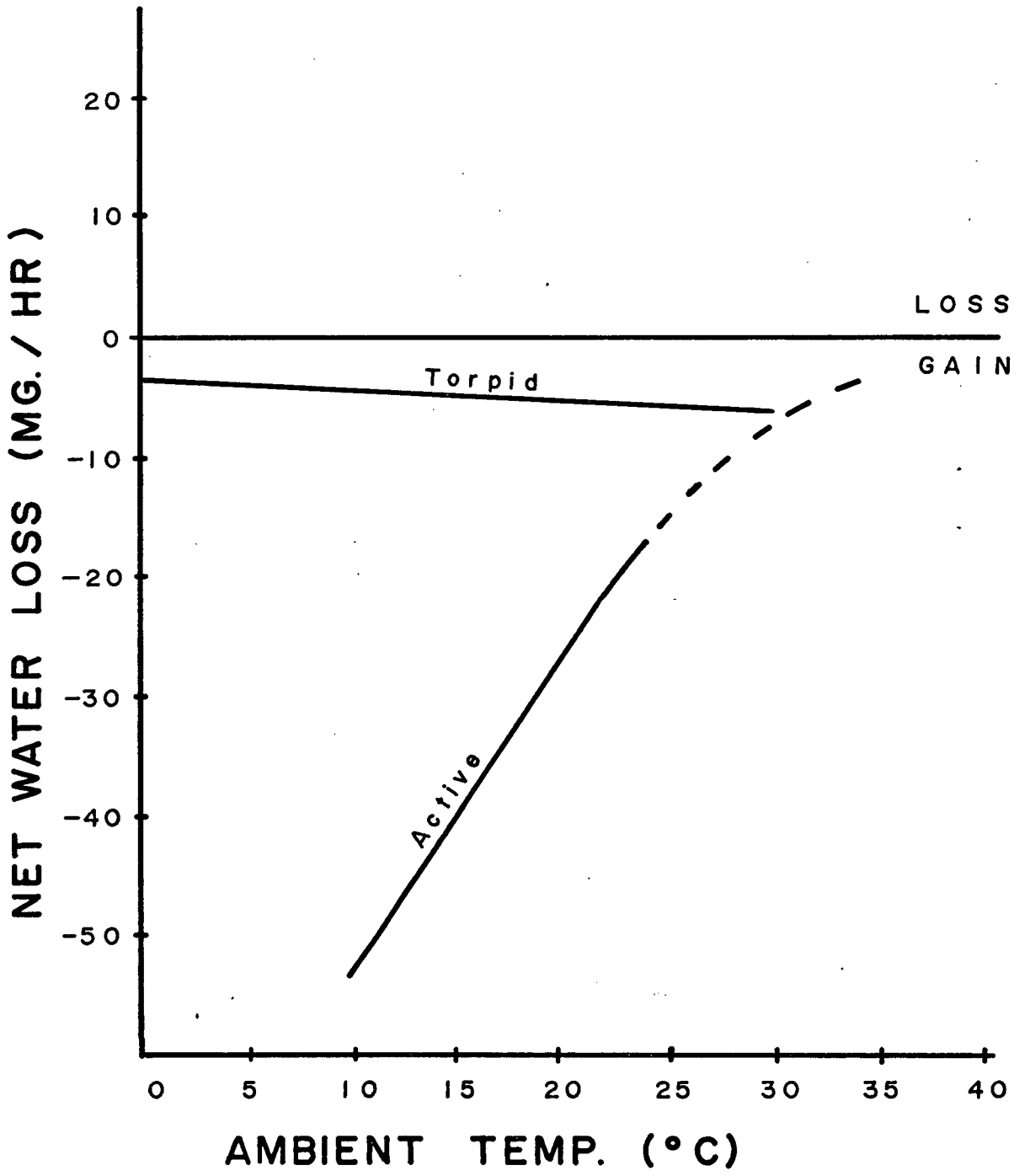


FIG. 38 ESTIMATED NET WATER LOSS OF ACTIVE AND TORPID MICE UNDER FIELD CONDITIONS



the animal is in a positive water balance under both sets of conditions, so, as mentioned previously, it is unlikely that water balance is a severe problem for small, fossorial desert rodents, under field conditions. The concept of water shortage for these desert rodents is even less credible when one considers that some green vegetation is utilized, and that seeds stored at 100% relative humidity will contain considerable moisture. If there is a water shortage for these animals, it would be during the winter when the soil moisture is in the form of ice, and absolute humidity is low. It is also at this time that the animals may face an energy shortage. Although the cost, in terms of water, of conserving energy by torpor is very high at the low temperatures expected during the winter (Fig. 32), the three-dimensional plots of the water budget model (Figs. 27, 34, and 36) indicate that even the smallest animals are capable of maintaining positive water balance at low ambient temperatures.

MAJOR FINDINGS OF THE THESIS

It seems appropriate to summarize the main findings of this thesis and to discuss some of the implications of these findings.

The conclusions that may be drawn from this study are:

1. Torpor is expensive in terms of water and cannot be a water-conserving mechanism in *P. parvus*. Fig. 30 shows that the net water loss of torpid animals is greater than the loss of normothermic animals over the entire range of ambient temperatures. Fig. 38, which shows the estimated water loss of normothermic and torpid animals under field conditions, indicates also that torpid animals have a higher net water loss.
2. Torpor is an energy-conserving mechanism as indicated by a comparison of Figs. 1 and 2. The energy conserved by torpor at 10 C is approximately 90% of the normothermic value. Since torpor conserves energy and expends water, it is possible to relate the two parameters by expressing the cost of energy conservation as mg of water expended/kcal of energy conserved, as shown in Fig. 32. The cost of conserving energy by torpor is lowest at 20-30 C.

3. P. parvus is capable of maintaining a positive water balance under severe conditions of cold and dryness. Fig. 30 indicates that positive water balance could be expected up to 20 C at 0% relative humidity. In a realistic field situation, positive water balance seems certain at all ambient temperatures up to 30 C (Fig. 38). Since metabolic water is the major source of water, an adequate food supply is the main requirement for the maintenance of positive water balance.

Since a diet of dry pearl barley produces more metabolic water than is required by P. parvus to eliminate the urinary and fecal wastes, it is clear that the problem of water balance lies with the pulmocutaneous water loss, which is influenced strongly by humidity and temperature. Measurements of pulmocutaneous water loss over a range of environmental temperatures at 0% relative humidity show that positive water balance can be maintained below 20 C by normothermic animals. However, torpid animals experience a negative water balance at all temperatures from 10-30 C. This is a consequence of balancing a "fixed" loss (cutaneous loss) against a much reduced metabolic water production. This fixed loss makes it impossible for P. parvus to conserve water by torpor. Since metabolic water is

the ultimate source of water for desert rodents, it is more reasonable to consider energy as the limiting factor of greatest significance to desert rodents. Their adaptations for water conservation have left energy as the major limiting factor. Torpor, as an energy-conserving mechanism, is a means of exchanging one limiting factor (water) for another (energy) in order to achieve the most satisfactory adaptation of the whole animal to its environment at a given time.

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APPENDIX I

Source of data used in Figs. 16 and 17.

Body Wt.	Species	Source
8.2	*Perognathus longimembris*	Chew *et al.* 1967
13.0	*Microdipodops pallidus*	Brown & Bartholomew, 1969.
15.9	*Peromyscus crinitus*	McNab & Morrison, 1963.
17.4	*Peromyscus eremicus*	MacMillen. 1965.
19.1	*Peromyscus maniculatus*	McNab & Morrison. 1963
19.9	*Peromyscus e. eremicus*	"
20.9	*Peromyscus crinitus*	"
21.5	*Peromyscus e. eremicus*	"
22.0	*Perognathus californicus*	Tucker. 1965.
24.2	*Peromyscus maniculatus*	McNab & Morrison. 1963
33.2	*Peromyscus t. truei*	"
33.3	*Peromyscus t. gilberti*	"
34.7	*Dipodomys merriami*	Dawson. 1955.
39.5	*Perognathus hispidus*	Wang & Hudson. 1970.
45.5	*Peromyscus californicus*	McNab & Morrison. 1963
49.6	*Peromyscus californicus*	"
56.9	*Dipodomys panamintinus*	Dawson. 1955.
110.0	*Neotoma lepida*	Lee. 1963.
139.0	*Neotoma lepida*	Lee. 1963.
145.0	*Jaculus orientalis*	Kirmitz. 1962.

APPENDIX II

Computer Program for Three-Dimensional Energy and Water Budgets

```
// JOB                                                    GUTHRIE
// FOR
*ONE WORD INTEGERS
*IOCS(KEYBOARD,1132 PRINTER,UDISK,DISK)
      REAL N,NOR,NL
      DIMENSION Z(11),ZEX(11),IHT(503),XP(11),YP(16)
      DEFINE FILE 1(176,2,U,IDN1),2(176,2,U,IDN2)
      IN=6
      IO=3
      IX=11
      IY=16
      N1=1
      N2=2
      NIHT=503
      RYY=1.0
      RZZ=0.3
      ABOUT=30.0
      ABOVE=30.0
      XSIZE=5.0
      YSIZE=5.0
      C1=21.5
      C2=0.6
      C3=35.0
      C4=1.81
      C5=0.068
      C6=40.45
      C7=1.127
      C8=168.0
      C9=2.5
      C10=4.42
      C11=1.05
      C12=0.0306
      C13=0.000163
      C14=168.0
      C15=40.45
      C16=1.127
      C17=0.102
      WRITE(IO,100)C1,C2,C3,C4,C5,C6,C7,C8,C9,C10,C11,C12,C13,C14,C15,C1
     16,C17
100   FORMAT('1',3F6.1,F6.2,F7.3,F7.2,F7.3,2F7.1,F7.2/
     1F7.3,F8.4,F10.6,F7.1,F7.2,2F7.3)
1     READ(IN)W,N
      IF(W*N)3,3,2
2     DX=14.0/N
      WRITE(IO,101)W,N,DX
101   FORMAT(//F6.1,F6.0,F6.2/)
      IDN1=1
      IDN2=1
      Y=-2.0
      DO 11 J=1,IY
      Y=Y+2.0
      X=-DX
      DO 10 I=1,IX
      X=X+DX
      ENT=N*W*(C1-C2*Y)
      ARO=N*W*(C3-Y)
      TOR=N*W*X*(C4+C5*Y)
      NOR=W*(C6-C7*Y)*(C8-N*X-C9*N)
      TCPW=ENT+ARO+TOR+NOR
      NL=N*X*(C10*C11**Y)+(C12+C13*Y*Y)*(C14-N*X)*W*(C15-C16*Y)
```

```
      TNL=NL-C17*TCPW
      Z(I)=TCPW
10    ZEX(I)=TNL
      WRITE(IO,102)Z,ZEX
102   FORMAT(5E12.4/6E12.4/5E12.4/6E12.4/)
      CALL DIDLW(N1,IDN1,Z,IX)
11    CALL DIDLW(N2,IDN2,ZEX,IX)
      CALL SCALF(1.0,1.0,0.0,0.0)
      CALL PERS(IX,IY,RYY,RZZ,ABOUT,ABOVE,XSIZE,YSIZE,XP,YP,Z,ZEX,N1,IDN
     11,IHT,NIHT)
      CALL PENUP
      CALL FPLOT(0,0.0,5.0)
      CALL SCALF(1.0,1.0,0.0,0.0)
      CALL PERS(IX,IY,RYY,RZZ,ABOUT,ABOVE,XSIZE,YSIZE,XP,YP,Z,ZEX,N2,
     1IDN2,IHT,NIHT)
      CALL PENUP
      CALL FPLOT(0,9.0,-5.0)
      GO TO 1
3     CALL EXIT
      END
// XEQ
```